

HOW DO MEASURES OF WATER QUALITY AND WATERFOWL POPULATIONS DIFFER  
BETWEEN NATURAL LAKES AND RESERVOIRS?

By

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A THESIS

Submitted to  
Michigan State University  
in partial fulfillment of the requirements  
for the degree of

Fisheries and Wildlife—Master of Science

2023

## ABSTRACT

While it is understood that reservoirs as a group are more highly connected to natural lakes, are located in warmer areas with increased precipitation, and experience more effects from land-use intensification and agricultural activities, it is unknown how water quality and biotic populations compare between these lake types. In chapter one, we studied 3,286 natural lakes and reservoirs ( $n = 1,514$  and  $1,772$ , respectively) over a 20-state extent in the midwestern and northeastern US. The limnological data was from the LAGOS research framework (LAke multi-scaled GeOSpatial and temporal). We built six generalized linear models (GLMs) to understand patterns and drivers of lake water quality. Compared to natural lakes, we found that reservoirs had significantly higher total phosphorus and chlorophyll-*a* concentrations, and significantly lower water clarity. We also found that the key driver lake maximum depth, as well as surface water connectivity, watershed cultivated cropland, watershed urbanization, and temperature were often significant predictor variables. In chapter two, we combined LAGOS data with that of ten species of in the Atlantic Flyway Breeding Waterfowl Survey from the United States Fish and Wildlife Service (spanning 21 years and 11 states). We compared population densities of the ten waterfowl species and built presence/absence models ( $n = 336$ ) to understand which species were more likely to be found in natural lakes or reservoirs. For the subset of lakes with driver variables ( $n = 135$ , 91 reservoirs), we also built quasi-Poisson generalized linear models (GLMs) to understand patterns and drivers of waterfowl population densities. We found that seven waterfowl species did not differ by lake type. However, wood duck and mallard population densities were larger in reservoirs. We also found that mallards and wood ducks were more likely to be present in reservoirs as compared to natural lakes but that common mergansers were less likely to be present in reservoirs as compared to natural lakes. We also examined population densities of wood ducks, mallards, and common mergansers over time and found that mallard populations decreased and wood ducks increased in both RSVRs and NLs from 2000-2021, whereas common mergansers increased in NLs and decreased in RSVRs. Finally, our models revealed that chlorophyll-*a*, region, climate, morphometry, connectivity, and land use/cover were predictive of waterfowl population densities, although all of these predictors were species-dependent. This study improves understanding of which lake type has better water quality and larger waterfowl populations, and which predictor variables may be driving these results. This study demonstrates that a combination of drivers working at multiple scales may lead to significantly poorer water quality in reservoirs. We also found two species that may prefer reservoirs and one that may prefer natural lakes, as well as species-dependent change over time. Therefore, this research can inform future decisions regarding management and conservation of reservoirs for water quality and waterfowl populations.

## ACKNOWLEDGEMENTS

I would like to offer my acknowledgements to my advisor, Dr. Kendra Spence Cheruvelil, and my graduate committee members – Dr. Patricia Soranno and Dr. Dana Infante of Michigan State University and Bradley Potter of the United States Fish and Wildlife Service. I would also like to acknowledge Patrick Hanly for immense assistance with coding, data analysis, and figure making, and Anthony Roberts of the United States Fish and Wildlife Service for providing the Atlantic Flyway Breeding Waterfowl Survey data that served as the foundation for the second chapter of this thesis. Additionally, I would like to acknowledge several members of my research lab – Ian McCullough, Nicole Smith, and Danielle Matuszak – for their assistance and support throughout this process. Finally, I offer my sincere thanks to my family for continuing to believe in me and for their unwavering support through my time in graduate school at Michigan State University. Funding to support my graduate studies came in the form of a teaching assistantship from the Lyman Briggs College, a research assistantship supported by the National Science Foundation (DEB 1638679), and summer support from the College of Agriculture and Natural Resources.

TABLE OF CONTENTS

CHAPTER ONE: HOW DOES WATER QUALITY COMPARE BETWEEN NATURAL LAKES AND RESERVOIRS?..... 1

    INTRODUCTION ..... 1

    METHODOLOGY ..... 8

    RESULTS ..... 13

    DISCUSSION ..... 20

    CONCLUSION..... 26

CHAPTER TWO: HOW DOE WATERFOWL POPULATIONS COMPARE BETWEEN NATURAL LAKES AND RESERVOIRS?..... 28

    INTRODUCTION ..... 28

    METHODOLOGY ..... 32

    RESULTS ..... 41

    DISCUSSION ..... 49

    CONCLUSION..... 55

LITERATURE CITED ..... 57

## CHAPTER ONE:

### HOW DOES WATER QUALITY COMPARE BETWEEN NATURAL LAKES AND RESERVOIRS?

#### **INTRODUCTION**

Myriad environmental factors influence both the overarching stability and the long-term health of our dynamic planet and its systems. Freshwaters and the aquatic communities that they support are one such highly complex system. In particular, lakes are considered sentinels of global climate change because they are sensitive to atmospheric and terrestrial changes (Adrian et al. 2009). Lakes also tend to reflect environmental changes that occur in the surrounding landscape and are thus indicative of landscape disruptions (Pham et al. 2008, Adrian et al. 2009, Soranno et al. 2010). For example, natural and anthropogenic catchment characteristics may affect not only the health of a lake, but may also reflect its response to changes in climate (Adrian et al. 2009). These landscape and climatic features can have direct and indirect effects on lake abiotic and biotic properties.

Many lake properties are negatively affected by such landscape and climatic disruptions (Adrian et al. 2009, Soranno et al. 2010). For example, land use and agricultural activities can cause nutrient loading and contamination from pesticide and fertilizer treatments (Álvarez et al. 2017). Such disturbances can increase suspended solids, contaminants such as atrazine or polychlorinated biphenyls (PCBs), and nutrient levels such as total nitrogen (TN) and total phosphorus (TP) (Williamson et al. 2008).

My research is concerned with anthropogenic increases in nutrients. TN and TP are necessary as the base of lake food webs, powering productivity (Walker et al. 2007) through autotrophs (for example, submerged aquatic vegetation (SAV) or pelagic algae). However, in excess, they cause cultural eutrophication, defined as a surplus of nutrients due to human activities, and can lead to a plethora of lake health issues (Walker et al. 2007). For example, declines in lake biodiversity can be catalyzed by oxygen depletion and the development of anoxic zones caused by eutrophication (Williamson et al. 2008). Cultural eutrophication and subsequent changes to lake water quality is cause for growing concern due to the multitude of disruptions they pose to freshwater ecosystems.

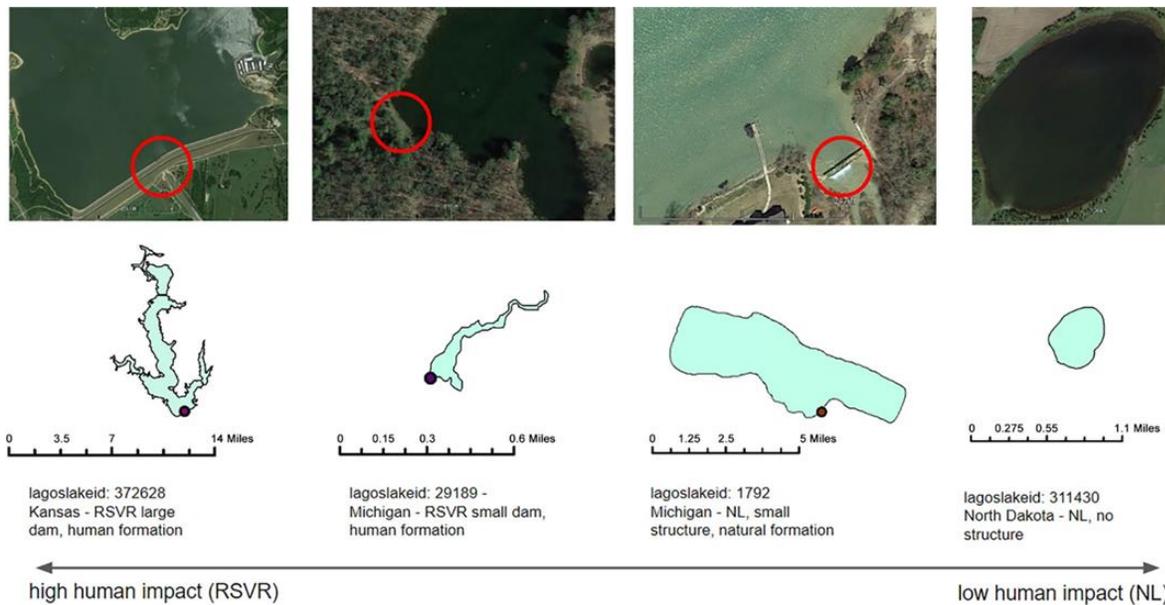
#### **A Comparison of Lakes and Reservoirs**

Although growing emphasis has been placed on understanding broad-scale lake responses to climate change and land use intensification, the majority of these studies have focused on either natural lakes (e.g., those in the relatively pristine northern regions of the US and Europe) or very large lakes globally, or they have not differentiated natural lakes from reservoirs. Although 'lakes' vary in degree of surface water connectivity, ranging from completely isolated to highly connected, and in degree of human

modification, ranging from completely natural to completely human-made, limnologists have long recognized the differences in form and function between lakes and reservoirs (Kalff 2002). Therefore, when seeking to understand how ‘lakes’ are affected by disturbances, it is likely that our understanding will be greatly increased by broad-scale studies that take lake type (i.e., natural lake or reservoir) into consideration.

Although natural lakes and reservoirs share many characteristics (e.g., relatively still, vertical stratification, horizontal zonation, seasonal turnover; Walker et al. 2007), they also have critical differences. Reservoirs are typically constructed for flood control, water supply, or irrigation (Thornton 1990, Walker et al. 2007) and their flow-altering structures can negatively impact levels of sediments, nutrient transfer and energy flow, and biodiversity (Lehner et al. 2011). Reservoirs are typically warmer than natural lakes, and have larger watershed areas that may allow for greater accumulation of both sediment and nutrients from agricultural runoff and other anthropogenic influences (Knoll et al. 2003). Furthermore, reservoirs are more likely to have a characteristic dendritic shape, whereas natural lakes are rounder (Hayes et al. 2017). Finally, reservoirs are considered to be highly connected to other water bodies, receiving inflow from a few prominent tributaries (Walker et al. 2007). However, limnologists have traditionally understudied reservoirs and have previously not had a way to differentiate natural lakes from reservoirs at broad spatial scales, leaving many knowledge gaps about the importance of reservoirs in global cycles (e.g., carbon, water) and how they respond to climate change and land use activities.

My research compares levels of TP, chlorophyll-*a* (Chl-*a*), and water clarity between natural lakes and reservoirs. To do so, I use a recently-published database (LAGOS-US RESERVOIR) that classifies all lakes in the conterminous US > 4 ha into their respective lake types (natural lake or reservoir; Rodriguez et al. 2023). In this database, we define a reservoir (RSVR) as a lake that is either constructed by or has been significantly altered by humans and has a water-control structure meant for changing or disrupting the flow of water (Figure 1; Rodriguez et al. 2023). In contrast, a natural lake (NL) is a water body that is naturally formed and either has no human interference, does not have a large, flow-altering control structure, or has a small human-made control structure that regulates water levels rather than altering water flow (Figure 1; Rodriguez et al. 2023).



**Figure 1.** Images and polygons depicting examples of two reservoirs (RSVRs, left) and two natural lakes (NL, right) that demonstrate critical visual differences between the two lake types. From left to right: a highly-modified and human-impacted lake with the presence of a large dam contributing to the characteristic dendritic shape of this reservoir, a less modified lake with a dam located on an incoming stream resulting in a reservoir, a natural lake that includes a water-level control structure at one location, and a natural lake with no water-level control structure that is characteristically round in shape. From: Rodriguez et al. 2023.

### Understanding Lake Water Quality

We studied three commonly-measured aspects of lake water quality: the limiting nutrient phosphorus (TP), a measure of pelagic algal biomass (Chl-*a*), and a measure of deep-water clarity (WC, commonly measured as Secchi disk depth). Phosphorus is typically considered vital to aquatic ecosystems (Walker et al. 2007). It is utilized by organisms for production and burning of energy in the form of ATP and is an important component of the genetic material DNA (Walker et al. 2007). Phosphorus typically enters lakes from both natural sources (such as rock weathering, animal waste, and organic tissue decay) and human-made sources (e.g., industrial effluents, surface runoff containing fertilizer, livestock waste) (Walker et al. 2007). Within lakes, phosphorus is usually found within the bodies of organisms, suspended in the water column, or attached to floating particles (Walker et al. 2007). Phosphorus is transferred between organisms via consumption, is often incorporated into the tissues of rooted plants to be used for energy, and can be deposited or released from lake-bottom sediments (Walker et al. 2007). Additionally, TP concentration often predicts a variety of indicators of both water quality and ecosystem health such as phytoplankton biomass, prevalence of toxic phytoplankton blooms, anoxia, water clarity, and species diversity (Brett and Benjamin 2008).

TP fuels production in natural lakes and reservoirs, and levels of phosphorus and nitrogen (TN) often work in tandem to establish co-limitations on primary productivity (Filstrup and Downing 2017).

Often, the level of such production is measured as chlorophyll, a green pigment that aids in photosynthetic processes of primary producers (Walker et al. 2007). The predominant type of chlorophyll that is most commonly used by autotrophic organisms is Chl-*a*, which functions as both a light harvester and plays a role in electron transport in plant photosystems (Björn et al. 2009). Chl-*a* is the only type of chlorophyll that conducts oxygenic photosynthesis in all types of autotrophs (Björn et al. 2009). Thus, Chl-*a* is often used as an indicator of the amount of algae in aquatic ecosystems. Chl-*a* has the highest concentrations when levels of TN and TP are also elevated (Filstrup and Downing 2017). In previous studies of temperate lakes, Chl-*a* was predicted as a positive log-linear function of TP (Cheruvilil et al. 2022, Filstrup and Downing 2017, Wagner et al. 2014). This relationship suggests that an increase in TP levels should be correlated with an increase in Chl-*a* levels, thereby contributing to greater productivity within the NL or RSVR in question.

Negative effects of excess TP concentrations can arise through eutrophication of freshwater ecosystems (Smith 2009) linked to both anthropogenic disturbances and climate change (Glibert 2020). Excessive nutrient concentrations can lead to a wide variety of negative impacts, including significant changes in both the composition and biodiversity of wildlife, uninhibited proliferation of primary producers including harmful algal blooms (HABs), radical depletion of dissolved oxygen and eventual formation of hypoxic zones, pH fluctuations, presence of cyanotoxins and other toxicity issues, and increased risk to human health through contamination of drinking water (Gold and Sims 2005, Walker et al. 2007, Glibert 2020). Aquatic wildlife may face degraded water quality and clarity, toxicity resulting from microcystin and other cyanotoxins, hypoxia and anoxic zones, and alterations to food webs and energy flow (Walker et al. 2007, Chislock et al. 2013).

Increased TP and subsequent increases in Chl-*a* can also lead to decreases in lake WC, which is a desired state for lake users and property owners. WC is an excellent indicator of overall lake health, water quality, and trophic condition of freshwater environments (Peckham and Lillesand 2006). Furthermore, WC is particularly sensitive to changes in nutrient inputs as well as to rapidly warming climate conditions (Alsahli and Nazeer 2021). WC is also closely linked to the concentration of suspended sediments, dissolved organic matter, and chlorophyll, making it a critical variable to include when analyzing lake water quality (Alsahli and Nazeer 2021). Finally, WC is commonly sampled at broad spatial extents, due in part to the vast contribution and efforts of citizen scientists (Poisson et al. 2019), in order to study freshwater responses to environmentally disruptive events such as cultural eutrophication. Therefore, these WC data facilitate study of declining water quality and lake health at broad scales.

### **Factors Affecting Lake Water Quality**

Many natural and anthropogenic features affect nutrients, chlorophyll, and clarity in natural lakes and reservoirs. In fact, a wide range of natural and anthropogenic landscape and climatic features affect

lake nutrients and productivity (e.g., geomorphology, land use/cover, climate). In particular, lake depth and surface water connectivity can be important for understanding patterns of lake TP, Chl-*a*, and WC. However, due to the relative lack of research on reservoirs at broad scales, we know little about how these important lake and landscape features, and the factors that drive them, compare between NLs and RSVRs.

Geomorphology factors, such as lake total area, lake depth, watershed to lake area ratio (WS:LK), and lake shoreline development (measured as shoreline development factor; SDF) may play a role in lake water quality. For example, SDF can influence the frequency of resuspension a waterbody experiences. As the degree of fetch (the area over which wind blows while generating waves in a body of water, related to lake area and SDF) increases, so does resuspension of lake-bottom sediments and nutrients (Moses et al. 2011). However, lake depth is perhaps the most important of the geomorphological variables in influencing many lake physical, chemical, and biological processes (Kalff 2002) and thus improving predictions of lake nutrient and chlorophyll concentrations (Oliver et al. 2016). In particular, lake depth is an indicator of whether or not a lake will thermally stratify, which is related to whether or not oxygen depletion occurs in the hypolimnion. Lake depth can also directly affect resulting phosphorus concentrations after a water quality stressor event, which could include a variety of disturbances (Oliver et al. 2016). Additionally, lake depth affects P retention, which helps determine the extent to which internal P loads are processed (Stachelek and Soranno 2019). Shallower lakes are more prone to P recycling from lake-bottom sediments to the epilimnion and surface waters (Taranu and Gregory-Eaves 2008). They experience more frequent mixing in warmer months, redistributing sedimented phosphorus and causing more P recycling (Stachelek and Soranno 2019). This increase in P recycling suggests that shallower lakes are more susceptible to P retention and higher levels of TP in general. Thus, lake depth is not to be ignored when studying lake nutrient concentrations. Unfortunately, lake depth measurements are not common (Oliver et al. 2016, Stachelek et al. 2022, Webster et al. 2022) and are not well-estimated (Hollister et al. 2011, Oliver et al. 2016, Sobek et al. 2011).

Yet another important driver of water quality is hydrologic features such as the presence of dams, groundwater levels, and surface water connectivity. The presence of dams affects hydrology and these water-control structures can exert both negative and positive effects on nutrient concentrations. Dam construction may cause a buildup of nutrients and toxic algal blooms behind the dam itself, but one study has shown that dams may help to retain carbon and other critical life-building nutrients that may be otherwise lost due to soil erosion (Mongil-Manso et al. 2019). Groundwater recharge, a hydrologic process by which surface water replenishes underground sources and becomes 'groundwater', was found to affect algal blooms through changes to water chemistry (Brookfield et al. 2021).

Finally, the degree of surface water connectivity can affect lake water quality. For example, some studies have found that connectivity is a driving force behind the exchange of particulate and dissolved

matter, including both suspended sediments (which affect WC), nutrients such as TP, TN, and Chl-*a*, within aquatic systems (Fergus et al. 2017, Stachelek and Soranno 2019, Tockner et al. 1999). When surface water connectivity is greater, lakes may experience an influx of organic matter and nutrients from alternate sources that subsequently become accessible for primary producers and to aquatic wildlife (Tockner et al. 1999). Interestingly, other studies have found that upstream lakes can sometimes act as nutrient sinks, demonstrating the increased connectivity does not always lead to increased nutrients (Zhang et al. 2012). Other studies suggest complex interactions between connectivity and regional landscape features affecting lake water quality. For example, although lakes with high watershed wetland cover were found to have higher phosphorus levels in the majority of downstream lakes (Zhang et al. 2012), lakes with high watershed wetland cover in regions with high agriculture were associated with decreased levels of TP (Fergus et al. 2011). Thus, freshwater connectivity can affect nutrient concentrations in complex ways and should be considered when modeling water quality of NLs and RSVRs.

Studying the effects of surface water connectivity on lake nutrients can be challenging, as connectivity can be measured in many ways. For example, some studies use water residence time (i.e., the amount of time a drop of water stays in a lake) because that measure provides a deep understanding of nutrient retention and movement among waterbodies (Stachelek and Soranno 2019). However, water residence time requires stream gauges, making these data unavailable for most lakes and for broad-scale studies. Therefore, connectivity is often characterized according to surface water connectivity classes such as lake order or landscape position (e.g., Martin and Soranno 2006, Riera et al. 2000, Soranno et al. 1999). Studies have shown that lake response to external drivers varies according to these connectivity classes. For example, connectivity class was important for understanding the effect of land use/cover on lake nutrient influx (Soranno et al. 2015). In fact, connectivity classes captured differences in characteristics that can influence nutrient loading, such as upstream lake area, percentage of wetland cover, and catchment area. (Soranno et al. 2015). It is traditionally assumed that RSVRs, as a group, are more highly connected than NLs. However, this assumption is based on only one type of RSVR: run-of-the-river RSVRs. In fact, research studying the effects of connectivity on lake water quality have rarely focused on RSVRs, nor have they compared the effects of connectivity on water quality in NLs and RSVRs.

Along with lake depth and surface water connectivity, a wide range of natural and anthropogenic landscape and climatic features affect lake nutrients and productivity. In particular, land use/cover and climate have been shown to influence lake water quality. For instance, the expansion of urbanized areas (highly developed land including high road density) coupled with more intense phosphorus pollution from point sources (i.e. raw and treated sewage discharge), produced hypoxic conditions in over 1,500

watersheds (Jenny et al. 2016). Freshwaters are generally vulnerable to eutrophication in regions that experience high nutrient runoff or that undergo frequent and intensive land use from agricultural activities, such as crop-cultivated lands (Stachelek et al. 2020). However, recent studies have also shown that the relationship between agriculture and lake nutrient levels can vary depending on the ecological context of the waterbody. For example, research has demonstrated the importance of including both watershed land use and other lake-specific characteristics in lake water quality models (Collins et al. 2017, Fergus et al. 2017, Read et al. 2015, Stachelek et al. 2020).

Furthermore, climate features such as growing season length, precipitation levels, and annual mean air temperature have been found to significantly affect lake productivity and nutrient concentrations. For example, it was found that an increase in annual mean air temperature was related to an increase in algal biomass, and that the more eutrophic a lake was, the greater the effect that temperature had on the growth of algal blooms (Ye et al. 2011). Additionally, precipitation levels may affect relative productivity of lakes with a greater incidence of heavy precipitation events likely to lead to ‘episodic increases’ in nutrient and pollutant loading (Coffey et al. 2018). Furthermore, long-term changes in water quality variables like TP and Chl-*a* are associated with climate variables such as summer temperature and winter precipitation, and climatic variables can help predict overall lake nutrients and productivity (Collins et al. 2019, Oliver et al. 2017). Additionally, water clarity was found to be negatively correlated with increases in summer maximum temperatures and increases in summer precipitation levels (McCullough et al. 2019). Lakes were found to be sensitive to changes in air temperature and precipitation (Adrian et al. 2009), further supporting the idea that they are sentinels of ecological changes at the macroscale.

To understand broad-scale differences in water quality between NLs and RSVRs, it is essential to study large numbers of lakes across a large spatial extent and to account for regional patterns among lakes and in landscape and climatic drivers. In addition, previous research has shown that it is necessary to account for the fact that these drivers operate at multiple spatial scales. For example, when studying 2,319 lakes across 6 US states, drivers quantified at local and regional scales affected patterns of lake phosphorus and alkalinity (Cheruvilil et al. 2013). Similarly, natural and anthropogenic factors at the regional scale, such as mean temperature, urban land use, influenced lake carbon cycling processes, emphasizing the importance of considering regional settings when studying lake water quality (Lapierre et al. 2018). One way to account for such regional patterns is to include a regionalization framework such as ecological regions in studies to understand water quality, and its drivers, in NLs and RSVRs (Cheruvilil et al. 2013).

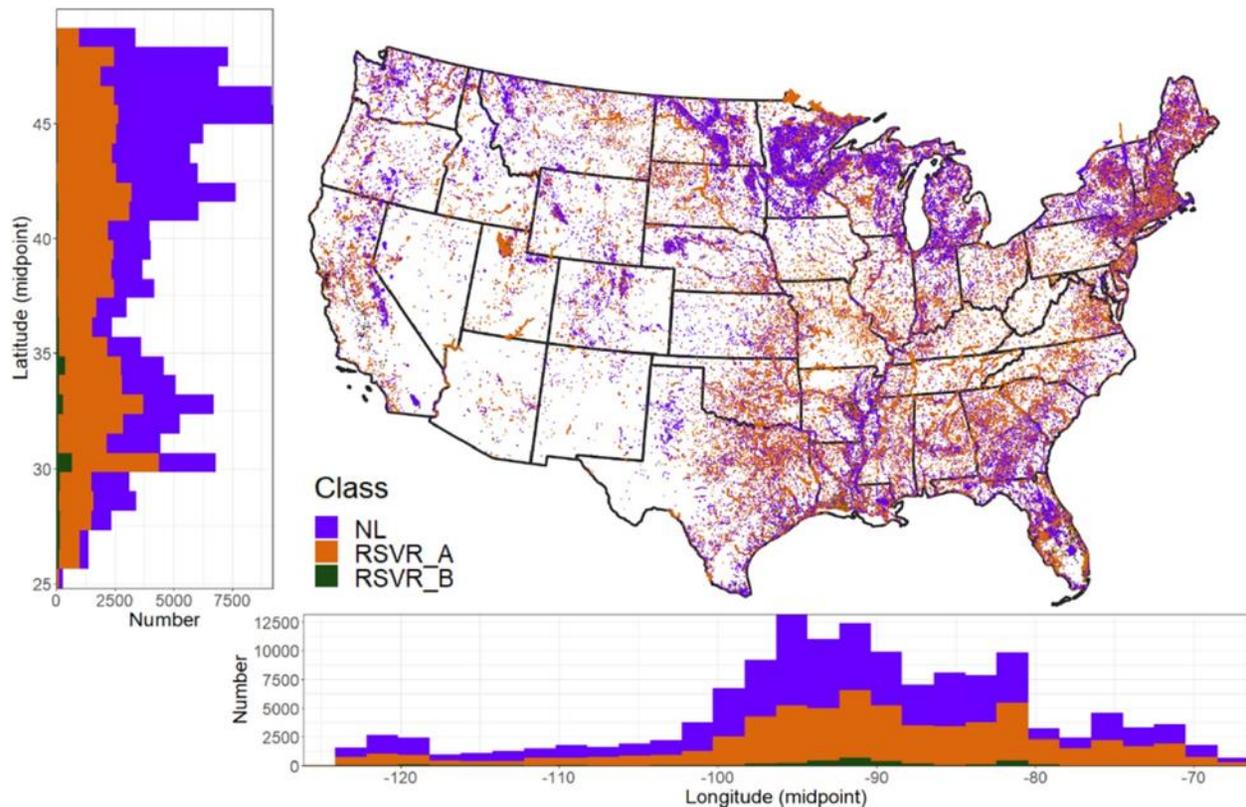
### **Research Questions and Expectations**

It is vital to understand how NLs and RSVRs differ in water quality and how they may respond differently to anthropogenic disturbances. We address this need by conducting a comparative study to

investigate the following overarching question: How do measures of water quality, and their drivers, compare between NLs and RSVRs? Specifically, we hypothesized that RSVRs will have higher concentrations of TP and Chl-*a* and will have lower WC than NLs. We predicted these differences based on conventional understanding of the human-made nature of RSVRs, as well as expected differences in landscape and climatic features that affect RSVRs as compared to NLs. For example, we expected RSVRs to be more common in southern areas of the US that are warmer and have more precipitation, to have higher levels of watershed land uses such as agriculture, and to have higher levels of surface water connectivity and watershed runoff as compared to NLs. We expected these characteristics would result in higher levels of TP and Chl-*a*, leading to diminished WC. To test this hypothesis, we took a data-intensive approach and studied broad-scale patterns of lake TP, Chl-*a*, and WC across wide ranges of lake depth, anthropogenic disturbances, and surface water connectivity.

## **METHODOLOGY**

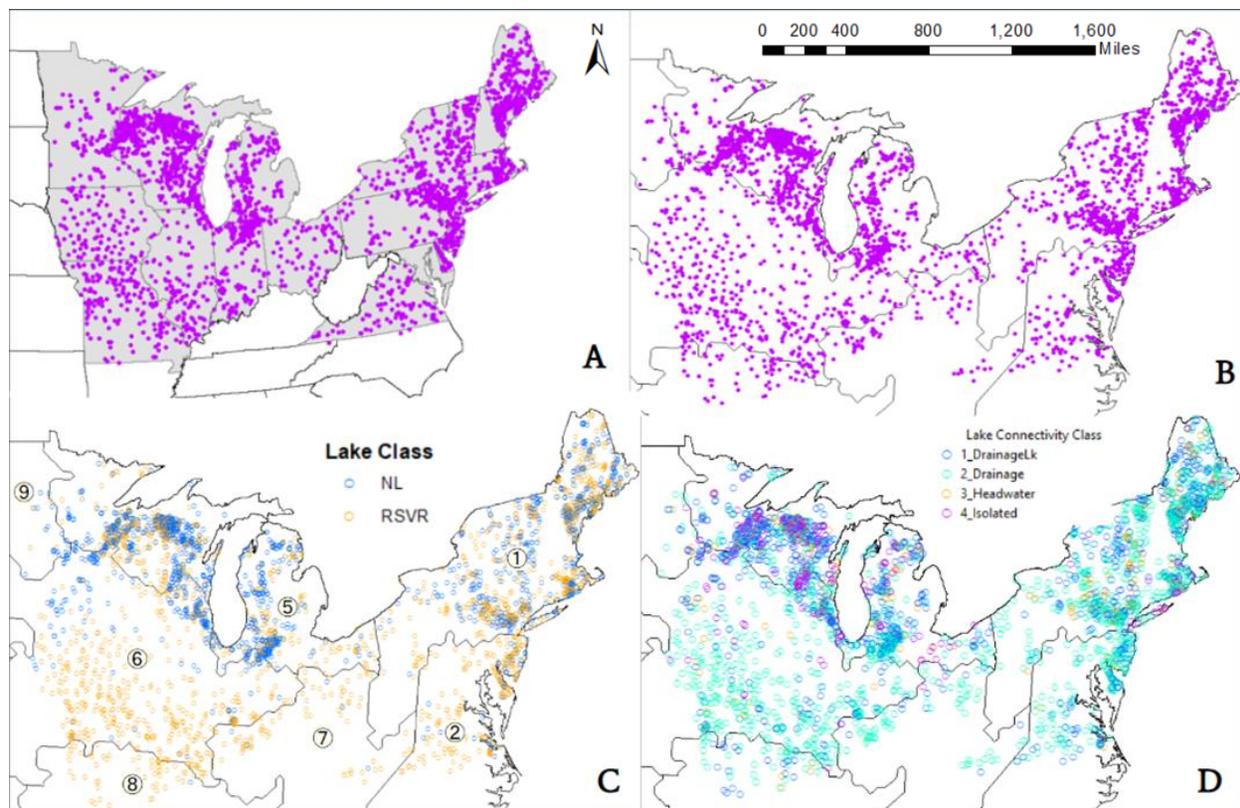
This research was made possible by the recent creation and publication of multiple modules for the LAke multi-scaled GeOSpatial and temporal (LAGOS) research platform that enables the macroscale study of the lakes in conterminous US (Cheruvilil et al. 2021, Soranno et al. 2015). In particular, the data module LAGOS-US RESERVOIR classifies all 137,465 lakes  $\geq 4$  ha in the conterminous US as either RSVRs or NLs (Figure 2; Rodriguez et al. 2023). The classification distinguished NLs from artificial RSVRs using a machine-learning predictive model and high-resolution imagery. The machine-learning model was based on the visual interpretation of lake outlines as well as a lake shape classification rule. A machine learning model was trained on 12,162 manually classified lakes and then used to predict NL or RSVR for the remainder of the lakes based on National Hydrography Dataset (NHD) Fcodes, lake isolation, and overall angularity. Angularity was chosen as one of the identifiers for reservoirs due to the fact that RSVRs are typically more dendritic in shape than NLs (Doubek and Carey 2017; Figure 1). This classification process resulted in 73,053 NLs and 64,412 RSVRs  $> 4$  ha in the conterminous United States (Figure 2; Rodriguez et al. 2023).



**Figure 2.** Map of LAGOS-US RESERVOIR and corresponding histograms showing the locations and class distribution of 137,465 lakes  $\geq 4$  ha as NL (purple,  $n = 73,053$ ), RSVR\_A (orange,  $n = 61,042$ ), or RSVR\_B (green,  $n = 3,370$ ) in the conterminous United States. ‘RSVR\_A’ refers to lakes that are likely human-made or human-altered by a large water control structure; ‘RSVR\_B’ refers to lakes that are likely human-made based on isolation and a shape rare in natural lakes. From: Rodriguez et al. 2023.

We then merged these data from RESERVOIR with water quality data from two other LAGOS data modules. First, we used the LAGOS-NE LIMNO data module that contains in situ data for TP, Chl-*a*, and WC from lake epilimnion (mixed, upper) layers (Soranno et al. 2017, Soranno et al. 2019). Second, we included in situ epilimnion TP, Chl-*a*, and WC measurements for three states (Virginia, Delaware, Maryland) that were not included in LAGOS-NE LIMNO, but are in LAGOS-US LIMNO (unpublished data). Merging these three datasets resulted in 3,286 study lakes that are in 20 northeastern and midwestern US states and seven ecological regions (NEON domains; Keller et al. 2008) (Figure 3). However, because there were only 4 lakes classified as RSVR\_B in this study dataset, we combined these with RSVR\_A. Epilimnion water quality data were filtered to meet four criteria that made sense ecologically and would facilitate model comparison across response variables. First, we selected recent years of sampling: 1997 - 2020. Second, data were filtered by the summer stratification period, or the phase of productivity during the summer months (June 15 to September 15, annually). Third, only lakes with data values for all three epilimnion response variables of interest (i.e. ‘complete cases’) were used.

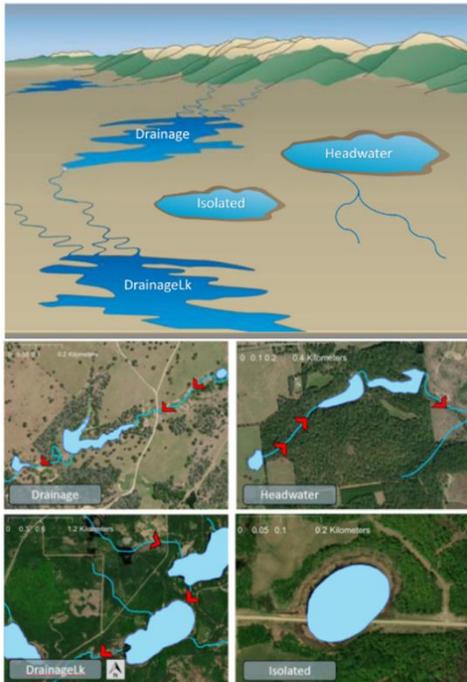
Fourth, for lakes that were sampled multiple times, we selected data from the most recent year ('maximum year').



**Figure 3. (A-D)** Study lakes ( $n = 3,286$ ) and study extent. A) The 20 US states (gray) and the study lakes (pink). B) The seven NEON regions and the study lakes (pink). C) The study lakes are classified as NLs (blue;  $n = 1,514$ ) or RSVRs (orange;  $n = 1,772$ ) within the 7 NEON regions, numbered 1, 2, 5, 6, 7, 8, and 9. NEON domains in the study extent are as follows: 1 = Northeast (NEON\_1), 2 = Mid-Atlantic (NEON\_2), 5 = Great Lakes (NEON\_5), 6 = Prairie Peninsula (NEON\_6), 7 = Appalachian and Cumberland Plateau (NEON\_7), 8 = Ozarks Complex (NEON\_8), and 9 = Northern Plains (NEON\_9). D) The study lakes are classified by connectivity class (1\_DrainageLk = 1,083, 2\_Drainage = 1,518, 3\_Headwater = 296, 4\_Isolated = 389). See text for definitions of connectivity classes. It should be noted that the lack of data points in New Hampshire is due to only 21 lakes having Chl-*a* in the initial LAGOS-NE dataset, so after filtering, there was no data left in the state that met all the constraints.

In order to study the factors that drive water quality in NLs and RSVRs, we supplemented these data with predictor variables from three other modules of LAGOS-US: GEO, LOCUS, and DEPTH. The LAGOS-US GEO module includes variables characterizing landscape features (e.g., agriculture, wetlands, hydrology, land use/cover, precipitation, temperature) at multiple time steps and at various spatial scales (e.g. watershed, the network watershed, region; Smith et al. 2021). LAGOS-US LOCUS contains additional variables that are likely to influence lake nutrient levels, such as lake total area and lake shoreline development factor (SDF, calculated by taking the ratio between the perimeter of a circle

with area equal to the lake area and the measured perimeter), lake connectivity (Cheruvilil et al. 2021, Smith et al. 2021), and NEON domains, which we use to account for spatial differences in response and predictor variables. Lake connectivity consists of four classes: Headwater, Drainage, Terminal, Isolated, DrainageLk, and TerminalLk (Figure 4; Cheruvilil et al. 2021). However, there were very few RSVRs (59) in the two terminal lake classes. Therefore, Terminal and TerminalLk classes were merged with Drainage and DrainageLk classes, respectively, to simplify this classification into the four classes of: Isolated, Headwater, Drainage, and DrainageLk, ranging from least to most connected, respectively. ‘Isolated’ lakes are those that lack both inflows and outflows, ‘Headwater’ lakes have an outflow but lack an inflow, ‘Drainage’ lakes have both inflow(s) and outflow(s) and lack upstream connected lake  $\geq 10$  ha in area, and ‘DrainageLk’ lakes have inflow(s), outflow(s), and have upstream connected lake(s)  $\geq 10$  ha in area (Figure 4; Cheruvilil et al. 2021). The final LAGOS-US data module used is DEPTH, which describes the observed mean (9,560) and maximum (17,700) depths of lakes and, for a subset of those lakes, includes information on lake bathymetry (Stachelek et al. 2021). We used lake maximum depth values rather than lake mean depth values as we had the most available data for lake maximum depth. Even so, there were 437 study lakes (141 = NL and 296 = RSVR) without lake maximum depth data.



**Figure 4. (A-E)** Cartoon depicting the four lake connectivity classes in LAGOS-US RESERVOIR (A; top) and aerial images (B-E) of the four classes used in this study (bottom; B-E). Image attribution: Esri, DigitalGlobe, GeoEye, i-cubed, USDA FSA, USGS, AEX, Getmapping, Aerogrid, IGN, IGP, swisstopo, and the GIS User Community. Symbols for diagrams courtesy of the Integration and Application Network ([ian.umces.edu/symbols](http://ian.umces.edu/symbols)) (Figure adapted from Cheruvilil et al. 2021).

<b>Predictor Variable (units)</b>	<b>Mean</b>	<b>Standard Deviation</b>	<b>Minimum</b>	<b>Maximum</b>
<b>Lake Total Area (ha)</b>	350.4	2748.5	4.0	121,898.7
<b>Lake Shoreline Development</b>	2.3	1.7	1.0	27.3
<b>Lake Maximum Depth (m)</b>	10.7	9.9	0.3	198.4
<b>WS Road Density (m/ha)</b>	33.8	26.5	0	266.9
<b>WS Dams (#/sqkm)</b>	0.03	0.2	0	6.9
<b>WS Wetlands (%)</b>	13.0	14.2	0	87.2
<b>WS Cultivated Crop (%)</b>	15.6	23.7	0	93.4
<b>WS Terrain Ruggedness Index</b>	1.8	1.2	0.1	8.3
<b>HU12 Baseflow Index (%)</b>	52.1	15.2	7.3	88.0
<b>HU12 Mean Temperature (°C)</b>	7.9	2.7	2.6	15.4
<b>HU12 Precipitation (mm/year)</b>	994.6	178.7	635.4	1501.5
<b>HU12 Runoff (mm/year)</b>	393.9	178.1	41.3	800.4

**Table 1.** Summary statistics (mean, standard deviation, range) of the non-transformed predictor variables for the 3,286 study lakes. The continuous predictor variables were quantified for each lake (area, SDF, depth), each lake watershed (WS; wetlands, dams, roads, cultivated crops, terrain ruggedness index), or the HU12 (USGS Watershed Boundary Dataset) for the few cases when the data source was too coarse (baseflow index, runoff, mean temperature, precipitation). Note that lake maximum depth has 437 missing values (n = 2,849) and that for wetlands, we combined emergent and woody wetland data.

The resulting dataset of NLs and RSVRs are spread across the US states and NEON domains, with highest numbers in the high-lake density northern parts of the study extent (NEON domains 1 and 5; Figure 3). Lakes are also represented in each connectivity class (Figure 4) and include a wide range of lake depth (Table 1). Finally, there are wide ranges of landscape and climatic predictor variables (Table 1), as well as the three water quality response variables (Table 2).

Response Variable (units)	Mean	Standard Deviation	Range
Total Phosphorus (ug/L)	46.1	80.1	0-1,120.0
Chlorophyll- <i>a</i> (ug/L)	20.4	37.7	0.03-573.0
Water Clarity (m)	2.5	2.0	0-17.4

**Table 2.** Summary statistics (mean, standard deviation, range) of the non-transformed water quality response variables for the 3,286 study lakes.

### Analytical Approach

We performed descriptive univariate exploratory analysis to identify missing values and any outliers that might unduly affect models, and to understand which predictor variables might be most likely to affect water quality in our dataset. Response (water quality) and predictor (driver) variables were either natural log (ln) or natural log +1 (ln +1) transformed to facilitate normal statistical distributions. Correlation matrices were used to understand correlated predictor variables and help us select variables to include in models. It should be noted that transformed variables measuring precipitation (mm/year) and runoff (mm/year) were both included in the final GLM, although they were highly correlated at  $r = 0.72$ . No other predictors were used if their correlations were  $> r = 0.55$ .

We used a group of six generalized linear models (GLMs) for analysis. We built a separate model for each of the three response variables: TP, Chl-*a*, and WC. Models were performed on standardized response variables (subtracted the mean and divided by the standard deviation) to aid in coefficient comparisons. We included continuous (Table 1) and categorical predictor variables in the models: lake type (RSVR as the standard), surface water connectivity class (most connected as standard; DrainageLk), and the NEON ecological regions (northeast US as standard; NEON 1). Because of missing lake depth data, we built two models for each response variable, one with and one without lake maximum depth as a predictor variable. This approach resulted in six total models to understand patterns and drivers of TP, Chl-*a*, and WC across the northeastern and midwestern US.

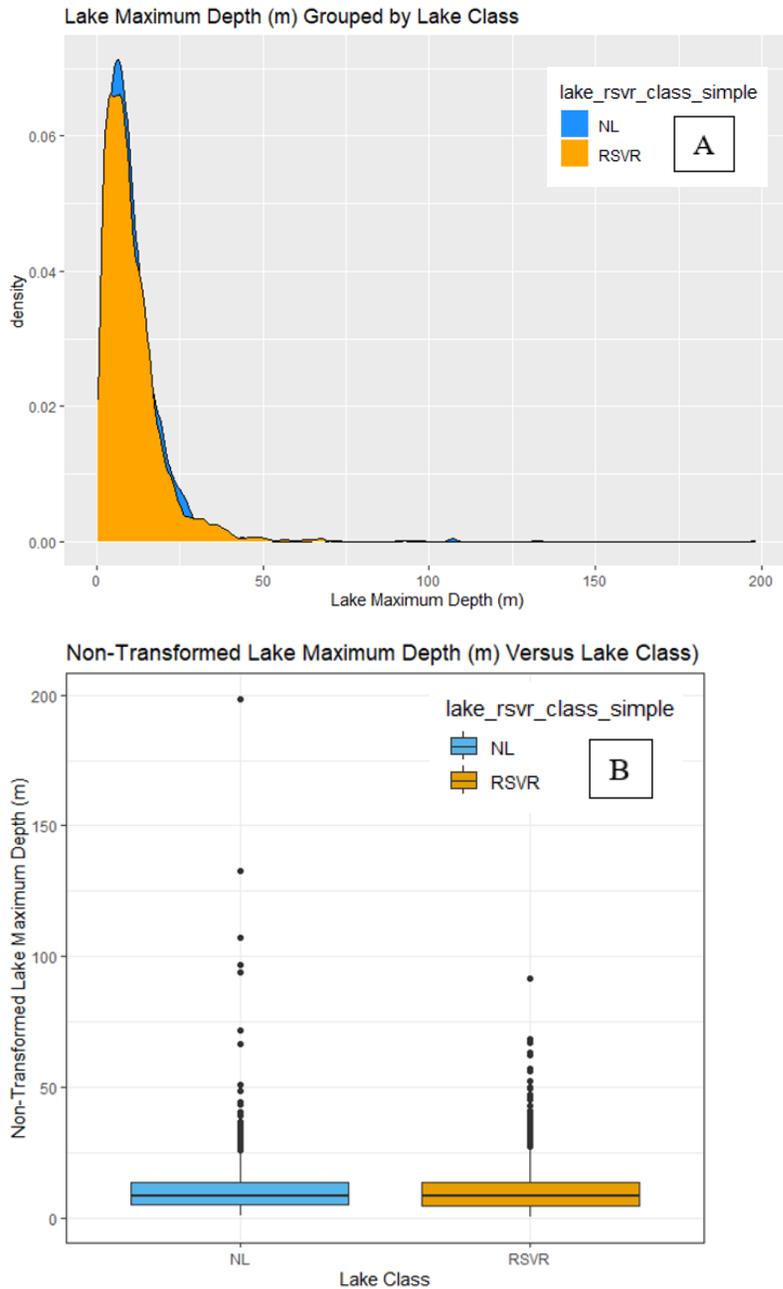
## RESULTS

Compared to NLs, we hypothesized that RSVRs would have higher concentrations of TP and Chl-*a*, and lower overall WC. Although we found some support for this hypothesis, it was not consistent across all models and depended upon whether (or not) the model included lake maximum depth (Table 3). For example, measures of water quality across the 20-state study extent were significantly different between the 1,514 NLs and 1,772 RSVRs in models without lake maximum depth, with TP and Chl-*a* concentrations significantly higher in RSVRs (Table 3) and WC significantly lower in RSVRs when compared to NLs (Table 3). However, lake type (NL vs RSVR) was not significant in models of 2,849

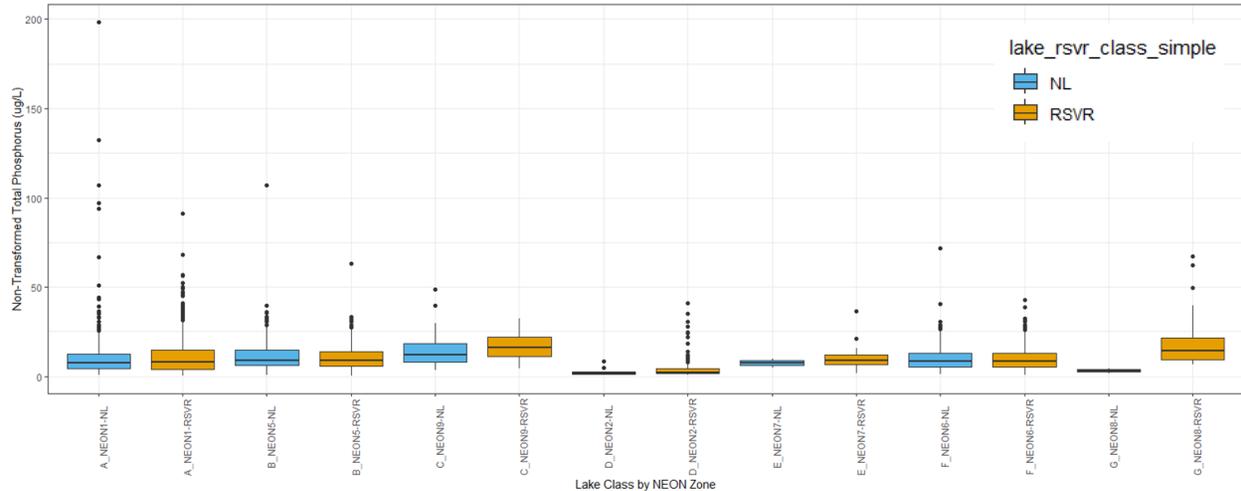
lakes with maximum depth data. When included in GLMs, lake maximum depth was always significant, with deeper lakes having lower concentrations of TP and Chl-*a* and higher WC overall (Table 3). Interestingly, lake maximum depth did not differ according to lake type (Figures 5, 6), leading us to assume that lake depth on its own is not driving these results and that something of greater complexity might be occurring.

	<b>Models With Lake Maximum Depth</b>			<b>Models Without Lake Maximum Depth</b>		
	<b>TP</b>	<b>CHL-A</b>	<b>WC</b>	<b>TP</b>	<b>CHL-A</b>	<b>WC</b>
<b>Slope</b>	3.5	2.4	1.1	3.6	2.6	1.0
<b>NEON: 1</b>	(**)-2, -8, -9; (*)-6, -7	-5*, -7**, - 9***,	-5**	(***)-2, -5, - 6, -8, -9	(***)-5, -6, -7, -9	(***) 5, 6, 9; 8**
<b>Lake: RSVR</b>	n/a	n/a	n/a	0.1*	0.1**	-0.05**
<b>Connectivity: DrainageLk</b>	-I**, -H*	-I***, -H*	I***, H*	-I***, -H**	-I***, -H**	I***, H*
<b>Lake Area</b>	0.1***	0.1***	0.04***	-0.1***	n/a	0.1***
<b>SDF</b>	0.05*	n/a	-0.03**	0.04*	n/a	-0.03**
<b>Max Depth</b>	-0.4***	-0.4***	0.3***	-----No Depth-----		
<b>Roads</b>	0.1, ***	0.05, *	-0.02, **	0.1, ***	0.1**	-0.03**
<b>Dams</b>	n/a	n/a	n/a	n/a	0.04*	-0.02*
<b>Runoff</b>	-0.2***	-0.2***	0.1***	-0.2***	-0.2***	0.1***
<b>Baseflow</b>	-0.3***	-0.4***	0.1***	-0.2***	-0.3***	0.1***
<b>Temperature</b>	0.2***	0.1**	-0.1***	0.2***	0.1***	-0.2***
<b>Precipitation</b>	-0.1**	-0.1*	n/a	-0.2***	-0.2**	0.1**
<b>Cultivated Crop</b>	0.2***	0.2***	-0.1***	0.2***	0.2***	-0.1***
<b>Wetlands</b>	n/a	n/a	- 0.05***	0.1***	0.1*	-0.1***
<b>TRI</b>	-0.1***	-0.1***	0.02*	-0.2***	-0.2***	0.1***
<b>Total R<sup>2</sup></b>	0.52	0.41	0.57	0.39	0.30	0.41

**Table 3.** Summary of generalized linear model (GLM) results modeling water quality response variables (TP, Chl-a, WC) as a function of many predictor variables characterized at multiple spatial scales. Models were run without (n = 3,286) and with (n = 2,849) lake depth as a predictor variable. Numbers in cells are model coefficients followed by p-values at levels of \*\*\* = 0.0, \*\* = 0.001, and \* = 0.01. ‘n/a’ indicates that a predictor variable was not significant in that model. Three categorical predictor variables were included in models (standard is listed in the predictor variable cell): NEON (7 Regions depicted as numerical domain codes as in Figure 3), Lake Class (RSVR or NL), Connectivity (4 Classes; I/H = isolated and headwater lakes, depicted in Figure 7). For these variables each cell includes any significant coefficients, whether it was + or -, and which classes were significant. TRI = Terrain Ruggedness Index, and SDF = Lake Shoreline Development Factor. Models were performed on standardized variables to aid in coefficient comparisons and transformations were performed when needed to meet statistical assumptions. See Table 1 for units of continuous predictor variables and Table 2 for units of response variables.

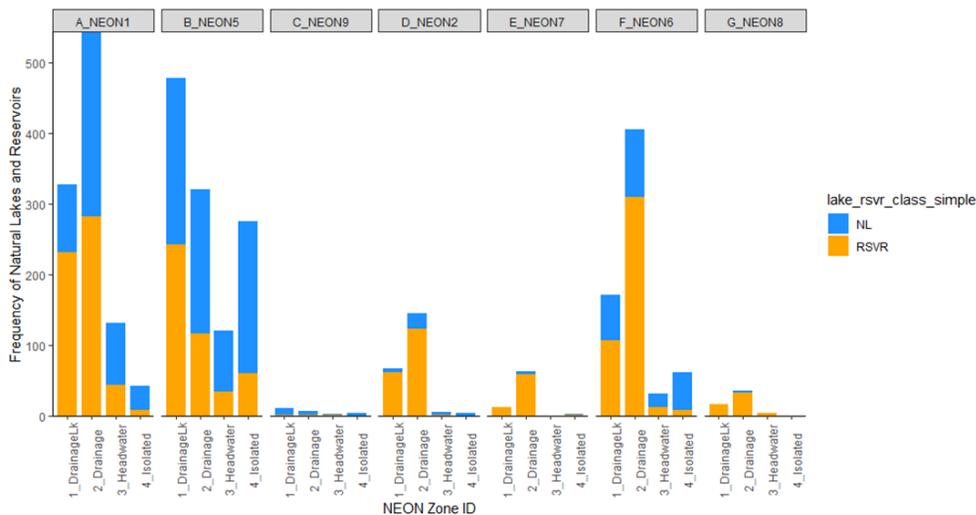


**Figure 5. (A-B)** A) Density plot showing the distribution of untransformed lake maximum depth by lake type (NL or RSVR) for the 2,849 lakes with lake maximum depth data. B) A boxplot showing untransformed maximum lake depth by lake type (NL or RSVR) for the 2,849 lakes with lake maximum depth data.



**Figure 6.** A boxplot of non-transformed lake maximum depth (in meters) by lake class (NL or RSVR) and NEON zone. NEON domains are ordered left to right starting with the ‘Northeast’ and ending with the southwest of the study extent (the ‘Ozarks Complex’).

The role of lake type in driving water quality is likely also affected by connectivity, which depends on ecological region. For example, we found some differences in the degree of connectivity between RSVRs and NLs that depended upon the NEON domain (e.g., most ‘Isolated’ lakes in the NEON domain 5; Figure 7). We also documented that RSVRs are more highly connected than NLs, with 62% of ‘DrainageLk’ and 61% of ‘Drainage’ lakes being RSVRs (Figure 7). In contrast, NLs dominate the ‘Headwater’ and ‘Isolated’ lake classes (68% and 80%, respectively; Figure 7). These patterns are born out in our models that demonstrated ‘Isolated’ and ‘Headwater’ lakes had significantly lower TP and Chl-*a*, and significantly higher WC than more connected lakes in all models (Table 3).

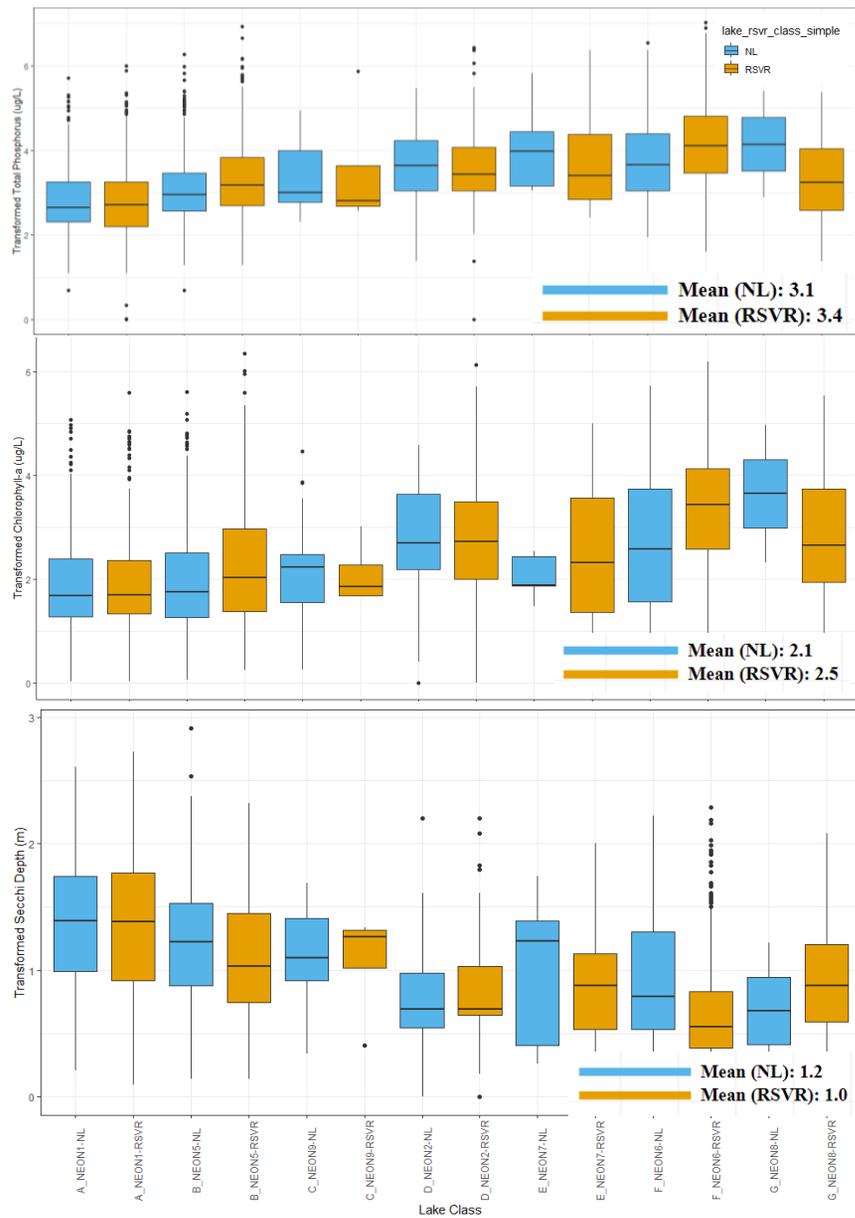


**Figure 7.** Frequency of NL and RSVR by the four lake connectivity classes, ordered from most connected on the left to most isolated on the right, and by NEON domain, ordered from the northeast to the

**Figure 7 (cont'd).**

southwest (See Figure 3 for map of NEON domains and see Figure 4 for description of connectivity classes). 'DrainageLk' n = 1,083, 'Drainage' n = 1,518, 'Headwater' n = 296, 'Isolated' n = 389).

We found differences in TP, Chl-*a* and WC based on ecological region, regardless of whether or not lake maximum depth was included as a predictor variable (Table 3). For example, TP was lower in NEON domains 2, 5, 6, 7, 8, 9 and Chl-*a* was lower in domains 5, 6, 7, and 9 (Table 3). However, the effect of ecological region varied depending on whether or not lake maximum depth was included as a predictor variable of water clarity. For example, we observed lower water clarity in NEON zone 5 when lake depth *was* included as a predictor, but significantly greater water clarity in NEON zones 5, 6, 8, and 9 when lake depth was *not included* as a predictor (Table 3).



**Figure 8.** A boxplot of transformed TP (top), Chl-*a* (middle), and WC (bottom) by lake class and NEON domain complete with averages for each lake class per NEON zone. Boxplots were also ordered left to right from the northeast to the southwest of the study extent. See Figure 3 for a map of NEON domains and see Figure 4 for description of connectivity classes.

In addition to lake type, lake connectivity, and ecological region, GLMs demonstrated the importance of landscape and climatic variables for understanding broad-scale patterns of TP, Chl-*a*, and WC. In many instances, some predictor variables were consistently significant across all models, for all three response variables, regardless of whether lake maximum depth was included in the model (Table 3). For example, watershed road density (meters per hectare) and cultivated cropland (percentage of land covered by cultivated crop) were consistently significant across all six models, with higher concentrations of TP and Chl-*a*/lower WC as road density and cultivated cropland increased (Table 3.) Additionally, runoff (mm/year) was positively associated with TP and Chl-*a* and positively associated with WC (Table 3). When baseflow index, mean temperature, and TRI increased, we saw subsequent decreases in concentrations of TP and Chl-*a*. However the effects of these three variables differed for WC, with an increase in WC for baseflow index and TRI, and a decrease in WC for temperature (Table 3).

Significance of a number of predictor variables also depended on the water quality variable itself (TP, Chl-*a*, or water clarity) and/or whether or not lake maximum depth was included as one of the drivers of water quality (Table 3). For example, although there was a positive association between lake area and both TP and Chl-*a* when lake depth was included, TP was negatively associated with lake area in models without lake depth (Table 3). Similarly, when lake depth was included in models, watershed wetlands were not associated with TP or Chl-*a* even though in models without lake depth we found significant positive associations between wetlands and both TP and Chl-*a*, along with a subsequent decline in WC. The coefficient for watershed dams was only significant in models without lake depth and for only Chl-*a* (positive) and WC (negative). Finally, the coefficient for precipitation was significant in models of all three water quality variables only in models without lake depth (Table 3).

## **DISCUSSION**

### **Drivers of Water Quality**

We found similarities in driver variables across the three water quality response variables. The variables that predicted TP were: lake type, lake connectivity class, NEON zone, lake maximum depth, SDF, lake total area, cultivated cropland, runoff, roads, TRI, baseflow index, precipitation, and mean temperature. The variables that predicted Chl-*a* were: lake type, lake connectivity class, NEON zone, lake maximum depth, cultivated cropland, runoff, roads, TRI, baseflow index, precipitation, and mean temperature. Finally, the variables that predicted WC were: lake type, lake connectivity class, NEON zone, lake maximum depth, SDF, lake total area, cultivated cropland, runoff, roads, TRI, baseflow index, wetland coverage, and mean temperature. Taken together, these results demonstrate the importance of lake type, lake connectivity class, ecological region, and a variety of morphological (especially lake maximum depth), landscape, and climatic variables for predicting lake water quality at broad scales.

## **Reservoirs**

We expected RSVRs to have higher concentrations of TP, higher concentrations of Chl-*a*, and lower levels of WC based on the inherently artificial, human-made nature of reservoirs (Lehner et al. 2011), along with previously established differences in both landscape and climatic features that influence RSVRs in comparison with NLs. For example, we expected RSVRs to have greater degrees of connectivity compared to NLs (Walker et al. 2007), to have more surrounding agricultural land (Knoll et al. 2003, Thornton 1990, Walker et al. 2007), and for RSVRs to be in warmer regions with higher levels of precipitation (Knoll et al. 2003). We expected a combination of these factors would result in higher concentrations of TP and Chl-*a*, followed by subsequent declines in WC. Our results were generally consistent with these expectations, with drivers such as lake connectivity, region, LULC (i.e. wetlands, urbanization, cultivated cropland, etc.), and climate producing significant water quality differences between NLs and RSVRs. Interestingly, in direct contrast to our findings, Doubek and Carey (2017) found that NLs were more eutrophic and had poorer water quality, measures by TP, Chl *a*, and WC, in comparison to RSVRs. There are multiple reasons as to why this study found different results as compared to our research. First, this study did not account for any connectivity classification and had no information regarding inflows, outflows, or landscape position (Doubek and Carey 2017). We know that lake connectivity is highly influential in determining nutrient content and water quality, so failing to account for a waterbody's connection to other freshwater sources may be impactful in trying to understand trophic states and overall water quality of NLs and RSVRs (Fergus et al. 2017, Stachelek and Soranno 2019, Tockner et al. 1999). Additionally, sampling of study lakes in the Doubek and Carey paper (2017) only took place in the year 2007, whereas our study spanned 23 years and examines trends in water quality and eutrophication over a much larger period. These sampling differences may result in drastically different results and may have been a primary reason for NLs having poorer water quality in the 2017 study (Doubek and Carey 2017).

## **Lake Depth and Chlorophyll-*a***

We also found that the influence of lake maximum depth on water quality affected those water quality differences by lake type. Extensive research has demonstrated the importance of lake depth for many internal processes that affect water quality. For example, lake depth affects phosphorus levels after a water quality stressor event (Oliver et al. 2016) and can influence the extent to which internal phosphorus loads are processed via controlling thermal stratification and benthic material resuspension in the water column (Stachelek and Soranno 2019). Additionally, shallower lakes, which experience more frequent mixing during warmer months (Stachelek and Soranno 2019), are more susceptible to phosphorus recycling from benthic layer sediments to the epilimnion (Taranu and Gregory-Eaves 2008). Interestingly, shallower and more connected RSVRs have been found to have greater nutrient

concentrations and higher light attenuation (Knoll et al. 2003), which aligns with our model results that demonstrated shallower RSVRs with greater connectivity had higher overall TP, Chl-*a*, and better WC.

Chl-*a* is used as an indicator of the amount of phytoplankton in aquatic ecosystems (Björn et al. 2009) and has been predicted as a positive log-linear function of TP (Cheruvilil et al. 2022, Filstrup and Downing 2017, Wagner et al. 2014). Lake depth is also negatively correlated with mean annual TP and Chl-*a* concentrations, which directly influence lake WC (Spears et al. 2013). This extensive research shows that lake depth plays a critical role in terms of lake nutrient concentrations, as well as in the consequential decrease in WC and the eventual formation of hypoxic zones, HABs, and organismal death. Interestingly, the significantly poorer water quality of RSVRs became insignificant in models run on the subset of lakes with lake maximum depth data, even though there was no significant difference in lake maximum depth between NLs and RSVRs. Perhaps these results point to NLs having other inherent features that are related to lake depth and enable the mitigation of nutrients pollution, making RSVRs more susceptible to eutrophication. Future lake sampling ought to include lake maximum depth so that this important feature is known for more lakes. Compared to water quality sample, there is much less lake depth data available (Oliver et al. 2016, Stachelek et al. 2022, Webster et al. 2022), and lake depths are not well-estimated (Hollister et al. 2011, Oliver et al. 2016, Sobek et al. 2011). Increased lake depth data will facilitate further research focused on understanding the effects of lake depth and lake type on water quality.

Finally, it is important to understand how our research, and its inclusion of lake maximum depth as an ecological driver of lake water quality, compares to pre-existing research comparing NLs and RSVRs. First and foremost, Hayes et al. (2017) found that lake depth can affect the processing rates of lake mass (water, solutes, particles), and that lake depth is a determinant of nitrogen retention in both NLs and RSVRs. Our results indicated that lake maximum depth is a highly influential driver of lake water quality between the two lake types, but that it likely works in tandem with a multitude of other ecological characteristics. Thus, Hayes et al. (2017) provides support for our findings, especially with regard to its effect on nitrogen retention in freshwater. Additionally, a study by Sjöberg et al. (2022) found that RSVRs and NLs exhibited morphometric differences in average depth. Our results, however, showed no significant difference in lake depths between the two water body types, which reiterates the idea that lake depth is not solely responsible for significant water quality differences between NLs and RSVRs. Finally, a study from Zhang et al. (2023) revealed water depth to be a key determinant of trophic state in waterbodies, affecting measurements of TP, WC, and total nitrogen (all of which are indicative of algal biomass in freshwater). These findings align with our results, demonstrating, once again, the critical role that lake depth, in combination with other ecological drivers, can play in determining overall water quality in NLs and RSVRs.

## **Lake Connectivity**

As expected, lake connectivity predicted lake water quality, and lake connectivity varies with lake type. TP and Chl-*a* concentrations increased, and WC decreased, as connectivity increased. For example, ‘Isolated’ and ‘Headwater’ lakes, which are least connected, had significantly lower nutrient concentrations and only included 685 RSVRs compared to the more connected connectivity classes that had higher nutrient concentrations and included 2,601 RSVRs. These hydrologic connectivity classes account for many variables that can be influential to nutrient loading, such as upstream lake area, catchment area, and percentage of wetland cover (Soranno et al. 2015). Since RSVRs in our study lakes and in previous research are more highly connected than NLs (Walker et al. 2007) and greater surface water connectivity may result in an influx of organic matter and nutrients (Tockner et al. 1999), RSVRs may be more susceptible to higher levels of TP and Chl-*a*. Our connectivity classes are based on surface water connections between and among lakes and streams. However, groundwater connectivity can also play a role in lake water quality. In fact, one index of groundwater, baseflow index, was significant in our models with a negative coefficient for baseflow index across TP and Chl-*a* models and a positive coefficient in WC models. This result may indicate that as the percentage of groundwater in a waterbody increases, it may upcycle groundwater with lesser nutrients back into the streamflow (Jordan et al. 1997). Therefore, it is important to consider lake connectivity, both surface and groundwater, in addition to lake type when studying and managing lakes.

## **Regional Influence**

We also found regional patterns in lake water quality, with lower TP and Chl-*a* and deeper WC in the northeast and higher TP and Chl-*a* and shallower WC in the southwest regions of our study extent. These same southwest regions have a dominance of RSVRs. For example, comparing the northeastern-most to the southwestern-most NEON zone, we find 54% as compared to 96% of lakes to be RSVRs, respectively. Our results are consistent with previous research that has found that some of the variation among lakes can be accounted for by ecological region (Cheruvilil et al. 2013) and that many factors that influence lakes and are linked to eutrophication processes (i.e. temperature, urban land use) also exhibit regional patterns (Lapierre et al. 2018, McCullough et al. 2019, Zhang et al. 2009). For example, winter precipitation and summer temperatures are important predictors of water quality (Collins et al. 2019) and these variables differ along longitudinal gradients. Thus, the fact that RSVRs have higher levels of precipitation (Knoll et al. 2003) and are abundant in southern regions where it is warmer shows the significance of taking into account ecological regions (i.e., NEON zones) when trying to understand and manage RSVR water quality. Furthermore, Doubek and Carey (2017) examined parameters that we did not explicitly consider in our research, such as latitude. However, this variable is essentially equivalent to examining the effect of regional influence, which we did consider with the incorporation of NEON zones

as a driver of lake water quality. This paper found that latitude is capable of affecting TP concentrations and Secchi disk depths, with NLs having higher TP and shallower Secchi depths at lower latitudes. In comparison, RSVRs had greater TP concentrations and shallower Secchi depths at higher latitudes, demonstrating that region and climatic conditions can be massively influential in determining water quality in these two water body types. While the water quality findings from Doubek and Carey 2017 do not directly correlate with ours, we did find that region was a significant driver of TP, Chl-*a*, and WC. This may indicate that specific latitudinal data is needed to understand the full extent of regional influence on water quality, and that RSVRs and NLs should be further examined to see how they behave according to region.

### **Land Use and Climate**

In addition to lake type, lake depth, connectivity, and region, measures of land use such as percentage of cultivated cropland and road density were consistently significant in our models. For both lake types, and more so for RSVRs, as the percentage of cultivated cropland and incidence of roads increased, we saw increases in TP and Chl-*a*, with subsequent declines in WC. It is well known that an increase in agricultural activity can lead to nutrient loading (Daniel et al. 1998, Torrent et al. 2007, Withers et al. 2007, Withers et al. 2014), and that this increase in nutrients and Chl-*a* can lead to reduced WC (Lathrop et al. 1996, McCullough et al. 2012). Additionally, urban ecosystems (those characterized by high levels of human activity and high nutrient inputs) may contribute to excess nutrient concentrations in aquatic ecosystems (Bernhardt et al. 2008, Carle et al. 2005, Walsh et al. 2005), and nutrient loads via stormwater drains in these urban ecosystems have been found to be primarily related to road density (Janke et al. 2017). Our results, also align with Williamson et al. (2008) and Knoll et al. (2003), in which they examine how anthropogenic influence can subsequently impact nutrient levels and WC in reservoirs.

Although few studies have explicitly studied differences between NLs and RSVRs, Hayes et al. (2017) synthesized differences between NL and RSVR characteristics within the context of predicting waterbody response to climate change. This research found that catchment and management characteristics are most crucial in mediating climate responses in RSVRs, and that a number of characteristics were different for RSVRs compared to NLs (e.g., position in landscape, shape, mass input, Secchi depth, and temperature). Interestingly, both Hayes et al. (2017) and our research revealed that RSVRs have greater nutrient concentrations, lower Secchi depths (lower WC), and warmer temperatures (Table 3).

Primarily, our research found that as temperatures increased, TP and Chl-*a* concentrations increased and WC declined. Increasing precipitation was associated with decreasing TP and Chl-*a* concentrations and improvement in WC. These results align with previous studies that have found

summer temperatures to act as strong predictors of lake nutrients and productivity (Collins et al. 2019) and have found temperature to influence primary production rates and stratification, which both exert influence on aquatic nutrient cycles (Collins et al. 2019, Kraemer et al. 2017). Additionally, we saw consistently significant decreases in TP and Chl-*a* as terrain ruggedness index increased, which supports the notion that steeper slopes facilitate inflow of freshwater that may not be contaminated by agricultural byproducts yet. Finally, Hayes et al. (2017) hypothesized that catchment and management characteristics would be more critical climate change mediators in RSVRs compared to NLs rather than temperature and precipitation, implying that RSVRs may be more susceptible to climate-related changes.

### **Research Limitations**

A few limitations in our research should be acknowledged because they restrict the generality of our results and represent opportunities for future research endeavors. First, the classification we used breaks up all lakes > 4 ha into the two classes of NL and RSVR (Rodriguez et al. 2023). However, we know that not all RSVRs are the same. In fact, LAGOS-US RSVR groups lakes into one of three groups (NL, RSVR-A, RSVR-B). RSVR-As are likely to be either human-made or highly human-altered by the presence of a relatively large water control structure that appears to significantly change the flow of water, whereas RSVR-Bs are likely to be entirely human-made based on a highly angular shape that is rarely, if ever, seen in natural lakes (Rodriguez et al. 2023). However, we only studied RSVR-As because there were very few RSVR-Bs within our study extent that had water quality data. Future research can build understanding about the patterns and drivers of the more highly-modified RSVRs as well as examine whether angularity affects water quality. Additionally, one could create a finer RSVR classification system that included other important differentiating factors (e.g., lake connectivity class). Including lake connectivity as part of a classification of RSVRs could enable further understanding of how connectivity can directly impact lake water quality, as well as how more ‘artificial’ ecosystems respond to ecological changes at the macroscale. Furthermore, our research was limited by the fact that some predictor variables were not normally distributed, even after transformation, and some variables may exhibit multicollinearity that may affect our results. Finally, while we did not find a significant difference in lake depth by lake type, we did not compare water quality response variables between NLs and RSVRs with similar lake maximum depth values, which could provide us with more insight on the relationships that may exist between lake depth, lake type, and water quality.

Very few studies, especially at the macroscale, have examined how natural lakes and reservoirs differ and how they may vary in their responses to land use intensification and climate change. Our research made use of a new RSVR classification for all lakes  $\geq 4$ ha in the conterminous U.S. (Rodriguez et al. 2023), which can be combined with additional broad-scale, in space and time, open-access datasets to study lakes and their drivers at macroscales to improve our understanding of RSVR water quality and its

drivers. For example, national-scale lake water quality databases (e.g., Hanly et al. forthcoming, Ross et al. 2019, Soranno et al. forthcoming) will allow researchers to examine whether the patterns we found hold across increasingly large ecological gradients of climate and land use and to examine how water quality has changed through time in RSVRs as compared to NLs.

### **Research Implications**

Our results can inform the understanding, management, and conservation of lakes. For example, our results lend support to the idea that RSVRs have lower water quality, which may indicate that they are susceptible to nutrient influx, pollution, and eutrophication events that could lead to HABs and aquatic ecosystem disruption. This may mean that natural resource managers and those making permitting decisions ought to be more conservative with RSVRs than NLs, and that future research should examine mechanisms underlying this pattern. We also found that a variety of lake and landscape predictor variables significantly impacted water quality (e.g., morphology, connectivity, land use, climate). Therefore, these features should be accounted for when implementing new policies and management practices to preserve the myriad ecosystem services RSVRs provide and to prevent water quality and biodiversity from experiencing declines.

### **CONCLUSION**

Reservoirs are extremely important in our society, providing drinking water, recreation, irrigation, and flood control. They are also very common, making up about 47% of the 137,465 total number of lakes  $\geq 4$  ha in the conterminous US. However, RSVRs are understudied compared to natural lakes. Conventional wisdom and past research says that these two waterbody types may be very different. For example, RSVRs may have increased susceptibility to nutrient influx, cultural eutrophication, and overall poorer water quality due in large part to their increased connectivity to other lakes (Oliver et al. 2016, Stachelek and Soranno 2019, Taranu and Gregory-Eaves 2008), their warmer temperatures (Knoll et al. 2003), their higher levels of precipitation and subsequent runoff (Knoll et al. 2003), and their inherently ‘artificial nature’ that allows them to be used for irrigation and flood supply (Thornton 1990, Walker et al. 2007). Additionally, with the presence of flow-altering structures that negatively impact sediment levels and nutrient transfer (Lehner et al. 2011), and larger watershed areas that expedite sediment and nutrient accretion from anthropogenic activities (Knoll et al. 2003), RSVRs may be more likely to be impacted by excessive nutrient concentrations and substandard water quality. In fact, results from our macroscale research support the idea that although waterbody type is important, it is not the whole story. Although we found that RSVRs, especially more connected ones, had significantly lower water quality in comparison to NLs when lake maximum depth was not included as a predictor, water quality did not

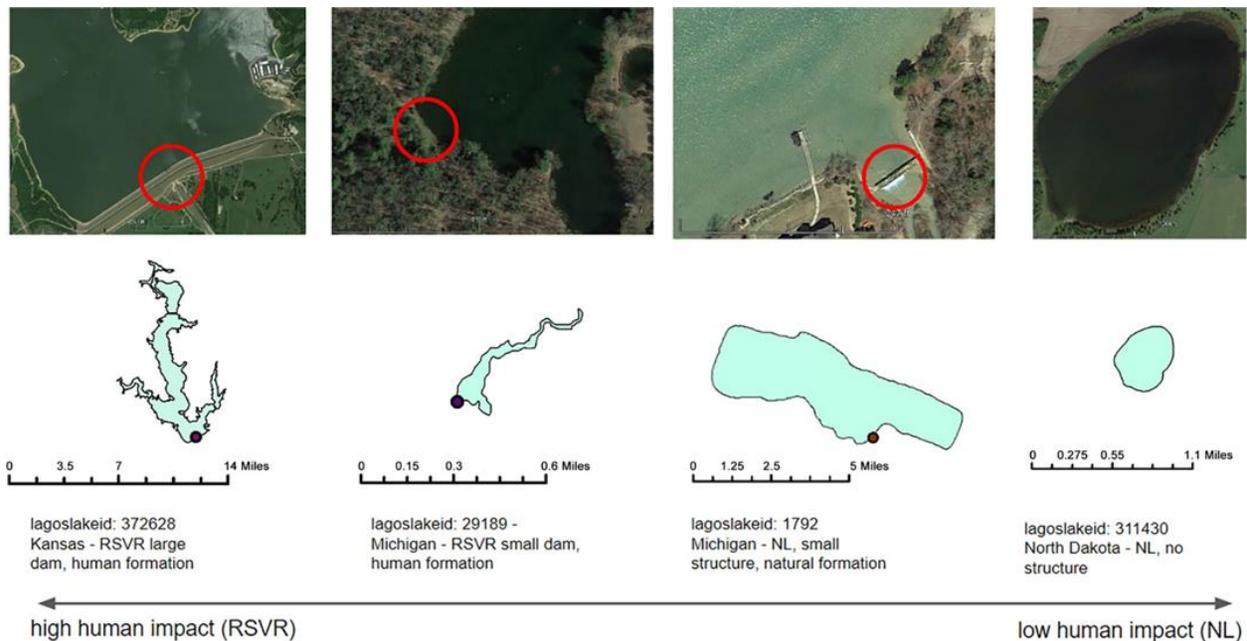
differ by lake type when lake maximum depth was included in models and a wide variety of landscape, climatic, and morphological drivers were also important drivers of water quality. Therefore, it is essential that researchers continue to include RSVRs when studying lakes to better understand them and how to better manage these important and common water bodies.

## CHAPTER TWO:

### HOW DO WATERFOWL POPULATIONS COMPARE BETWEEN NATURAL LAKES AND RESERVOIRS?

#### INTRODUCTION

The majority of freshwater research has focused on relatively pristine natural lakes (NLs), often in the northern regions of North America and Europe. This research has also not often differentiated between the two distinct lake types of NLs and reservoirs (RSVRs). In fact, there has not even been clear definitions for these two lake types. These facts have led to a relative dearth of knowledge about RSVRs and how they compare to NLs. In this research, we define a RSVR as a lake that is either constructed by or has been significantly altered by humans and has a water-control structure meant for changing or disrupting the flow of water (Figure 1, Rodriguez et al. 2023). In contrast, a NL is a water body that is naturally formed and either has no human interference, does not have a large, flow-altering control structure, or has a small human-made control structure that regulates water levels rather than altering water flow (Figure 1, Rodriguez et al. 2023).



**Figure 9.** Images and polygons depicting examples of two reservoirs (RSVRs, left) and two natural lakes (NLs, right) that demonstrate critical visual differences between the two lake types. From left to right: a highly-modified and human-impacted lake with the presence of a large dam contributing to the characteristic dendritic shape of this reservoir, a less modified lake with a dam located on an incoming stream resulting in a reservoir, a natural lakes that includes a water-level control structure at one location, and a natural lake with no water-level control structure that is characteristically round in shape. From: Rodriguez et al. 2023.

RSVRs are typically constructed for flood control, water supply, or irrigation (Thornton 1990, Walker et al. 2007) and possess flow-altering structures that may negatively impact sediment levels, nutrient transfer, and biodiversity (Lehner et al. 2011). In fact, research has shown that although NLs and RSVRs share many characteristics (e.g., relatively still, vertical stratification, horizontal zonation, seasonal turnover; Walker et al. 2007), they also have critical differences. RSVRs are typically warmer than NLs and have larger watershed areas that facilitate the buildup of both sediments and nutrients from agricultural activities (Knoll et al. 2003). RSVRs are also more likely to have a characteristic dendritic shape, whereas NLs are typically more rounded (Hayes et al. 2017, Figure 1). Finally, RSVRs have a greater degree of connectivity to other surface waters, receiving inflow from major tributaries (Walker et al. 2007).

RSVRs are common throughout the US (Hayes et al. 2017) and have myriad uses for both humans and wildlife alike. RSVRs have been used for thousands of years by human beings, and today are utilized for not only flood control and water supply, but for navigation, recreational purposes, and the generation of hydropower (Lehner et al. 2011). RSVRs are also critical for the success of wildlife, serving as habitat for a wide variety of organisms. For example, the term *waterfowl* encompasses birds that are found in aquatic habitats (Owen and Black 1990), such as lakes, reservoirs, and wetlands.

Waterfowl utilize both NLs and RSVRs for nesting sites, breeding and migratory grounds, and feeding (Batt et al. 1992, Owen and Black 1990). However, more research is needed regarding which ecological drivers, including lake type, are most likely to influence waterfowl population densities at the macroscale. This research helps to fill these knowledge gaps by combining existing waterfowl and lake data to answer the overarching question: how do waterfowl populations differ between NLs and RSVRs? Below, we describe waterfowl biology along with factors that potentially affect the success of breeding waterfowl, such as land use/land cover (LULC), climate, freshwater characteristics such as lake morphometry and water quality, and geographic location (i.e., region).

### **Waterfowl Biology and Factors Affecting Waterfowl Populations**

Many species of waterfowl create nesting sites adjacent to freshwater ecosystems, or build nests within emergent vegetation along banks (Batt et al. 1992). Waterfowl also use habitat in rivers, floodlands, inland deltas, and ephemeral waters (Owen and Black 1990). Furthermore, waterfowl have been observed using artificial wetlands, RSVRs, and riparian areas of shallow, eutrophic lakes for breeding and wintering. RSVRs can also create patches of still water in a previously flowing area that waterfowl use for nesting, breeding, and feeding (Owen and Black 1990).

There are many factors that can affect the waterfowl populations that rely on NLs, RSVRs, and surrounding wetlands. For example, typical factors that can affect breeding behaviors and survival of offspring include short-term weather events, growth of vegetation, and availability of sufficient nesting

sites (Owen and Black 1990). Other important factors affecting waterfowl include climate, lake characteristics, and landscape features that affect waterfowl habitat. Waterfowl are known to be sensitive to changes in land use and climate (Avilova and Eremkin 2019, Fernández et al. 2005, Lehtikoinen and Jaatinen 2013, Sorenson et al. 1998, Staniforth 2002). For example, climate changes such as drier conditions, increased evapotranspiration, warmer temperatures, greater potential for drought, and decreased wetland coverage reduce suitable habitat for waterfowl and can drive population changes (Sorenson et al. 1998). Furthermore, more frequently occurring drought conditions can lead to disrupted settling patterns, reduced clutch sizes, shortened breeding seasons, and lower brood survival (Sorenson et al. 1998). Winter air temperature changes and increased urbanization/human presence have also been linked with mallard (*Anas platyrhynchos*) population fluctuations (Avilova and Eremkin 2019). Finally, changes in climate (in the form of rising temperatures) and urban development encouraged migration overshoots (i.e., when migratory birds end up further than intended) in waterfowl (Staniforth 2002). Finally, certain species including the green-winged teal (*Anas carolinensis*) were more common within anthropogenic ecosystems as compared to natural ecosystems (Staniforth 2002).

Waterfowl breeding populations are also known to be affected by a whole host of freshwater characteristics, such as lake morphometry, pH, nutrient levels, and riparian zone wetland vegetation (Suter 1994). Lake features such as altitude, surface area, and morphology have also been found to influence the frequency at which some waterfowl species visit or spend time on lakes (DesGranges and Darveau 1985). For example, research has shown that waterfowl typically use islands as refuges from disturbance by mammals or other birds, and as a source of water, food, and nesting cover (Hammond and Mann 1956).

Land cover type, especially wetlands and protected lands, can also affect waterfowl populations. For example, waterfowl utilize riparian wetland environments for feeding and foraging, habitat space, and general refuge (Shaw and Fredine 1971, Stafford et al. 2011). However, wetlands are diverse and there are a variety of wetland characteristics that may be important for waterfowl. For example, wetland complexes may be used more by waterfowl than isolated wetlands (McKinstry and Anderson 2002). Mallards consistently selected wetland habitats that were part of sanctuary and wetland reserve areas (Beatty et al. 2014) and the creation of waterfowl reserves may result in larger duck populations (Mathevet and Tamisier 2002).

The geographic location, or region, that waterfowl inhabit may also help characterize populations. For example, Bird Conservation Regions (BCRs) are ecologically distinct regions across the North American continent that consist of similar bird communities, habitat composition, and resource management concerns (NABCI 2021). Previous studies involving BCRs and waterfowl populations have found that these regions can be helpful in determining population estimates for certain species (wood

ducks (*Aix sponsa*), for example)) and can be used to facilitate harvest and habitat management of waterfowl populations (Zimmerman et al. 2015). BCRs have also been used to forecast waterfowl population changes, including mallards, under changing climate conditions, highlighting the importance of spatial variation and density dependence in ecological regions (Zhao et al. 2016).

Finally, lake water quality may affect waterfowl populations, and vice versa. There may be a bi-directional linkage between water quality and waterfowl populations, especially when it comes to phosphorus and chlorophyll-*a*, a measure of open water algal biomass (Chl-*a*). Waterfowl are capable of degrading water quality through unintentional import of nutrients (Hoyer and Canfield 1994, Manny, Johnson, and Wetzel 1994). However, lake eutrophication can also produce desirable habitats for many waterfowl species (Hoyer and Canfield 1994, Kauppinen and Väänänen 1999). For example, one study found that waterfowl species were much more commonly found at nutrient-rich sewage lagoons and refuse dumps than they were in natural ecosystems (Staniforth 2002). Furthermore, in a study conducted of 20 Swiss lakes, both mean and maximum waterfowl species richness increased (especially for piscivorous waterfowl) with nutrient concentrations as systems transitioned from less-productive, oligotrophic lakes to more-productive, eutrophic lakes (Suter 1994). However, it is unknown whether these associations are mechanistic (or in what direction(s)), nor how the association differs for NLs compared to RSVRs.

### **Research Questions and Expectations**

This research seeks to understand how waterfowl populations compare between the lake types of NLs and RSVRs. Specifically, we ask: Do breeding waterfowl population densities differ by lake type?, 2) Are particular species more likely in NLs or RSVRs during the breeding period?, 3) Are breeding waterfowl population densities changing over time and according to lake type?, and 4) What climatic, lake, and landscape factors are associated with differences in breeding waterfowl densities between lake types?

We expected RSVRs to have significantly higher breeding waterfowl population densities than NLs based on our understanding of a) waterfowl biology and behaviors – including feeding and foraging behaviors, nesting, and breeding preferences – and b) RSVR characteristics that would attract waterfowl – including higher Chl-*a* concentrations and wetter, warmer climates. We expected some species-specific differences, such as more nuisance species (i.e., a species (native or non-native) that is capable of causing ecological or economic harm to a system) would be more likely in RSVRs and more rare species (i.e., species that are higher priority and may have a label such as ‘endangered’ on the International Union for the Conservation of Nature ‘Red List’) would be more likely in NLs (Rodrigues et al. 2006). We did not have any *a priori* expectations of how waterfowl populations have changed through time and by lake type since previous research has not been done on this question. Finally, based on the research summarized

above, we expected that a combination of lake, landscape, and climate features would be associated with waterfowl population densities (e.g., lake water quality, connectivity, lake type, wetland cover, protected areas, and climate).

To answer our questions, we took a data-intensive approach. We combined broad-scale existing datasets on lakes, landscapes, climate, and waterfowl. Our study population is 336 lakes across 11 US states and ten species of waterfowl for which we had data from a 21-year period (2000-2021). This research will allow us to better understand which ecological drivers, including lake type, are most influential in determining waterfowl populations at the macroscale.

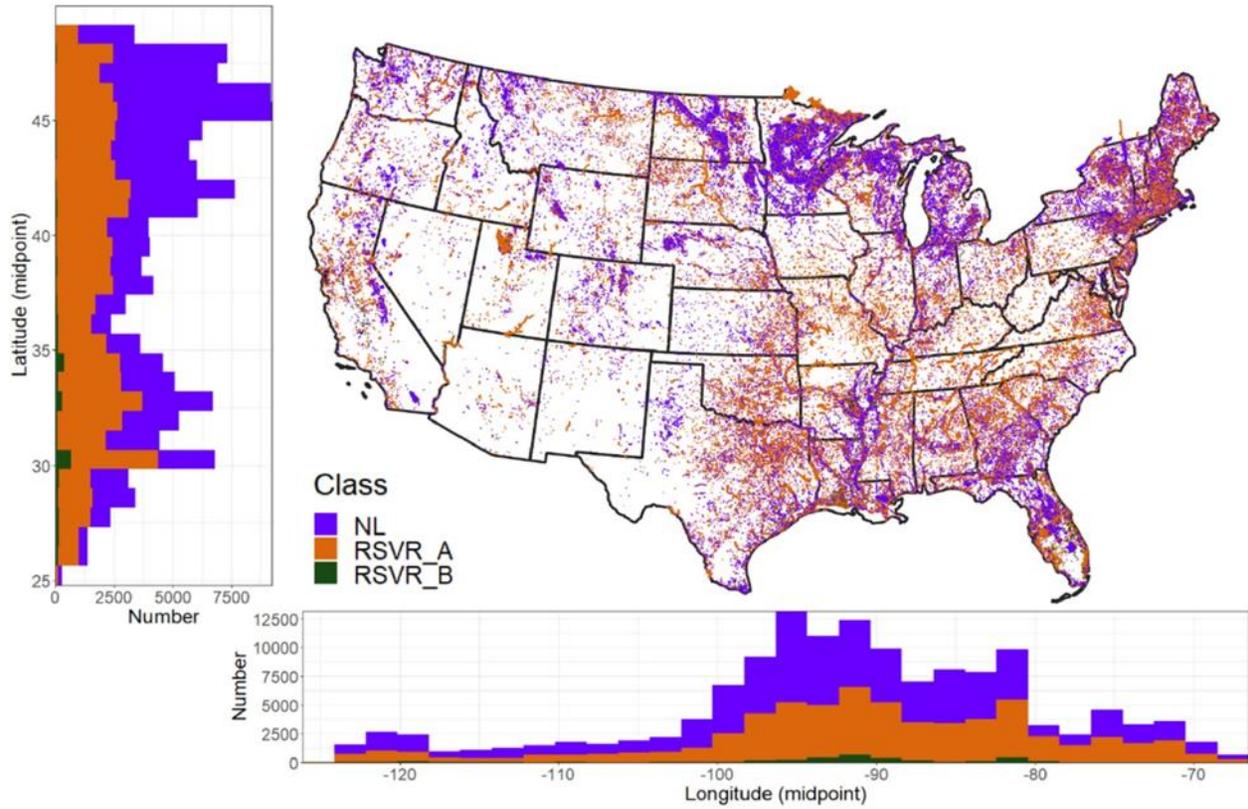
## **METHODOLOGY**

Our data-intensive approach utilized data from two main sources, one with data about lakes and their ecological contexts (i.e., LAke multi-scaled GeOSpatial and temporal (LAGOS); Soranno et al. 2015, Cheruvilil et al. 2021) and the other with data about waterfowl (i.e., the USFWS Atlantic Flyway Breeding Waterfowl Survey).

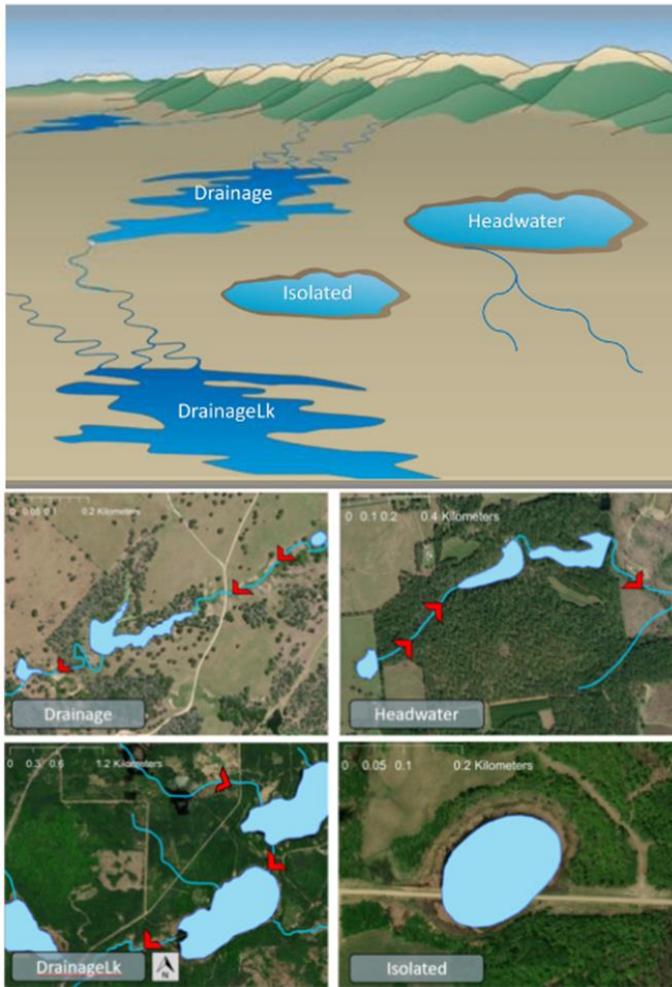
### **Study Lakes and Extent**

We made use of several data modules from the LAGOS research framework. The LAGOS-US RESERVOIR module classifies all 137,465 lakes  $\geq 4$  ha in the conterminous US as either RSVRs or NLs (Figure 2, Rodriguez et al. 2023). The classification distinguished NLs from artificial RSVRs utilizing a machine-learning predictive model and high-resolution imagery. In order to study the other factors that potentially drive waterfowl populations, we supplemented this LAGOS-US RESERVOIR data with predictor variables from three other modules of LAGOS-US: GEO, LOCUS, and LANDSAT. The LAGOS-US GEO module includes variables characterizing landscape and climatic features (e.g., agriculture, wetlands, hydrology, land use/cover, precipitation, temperature) at multiple time steps and quantified for various spatial scales (e.g., watershed, the network watershed, region; Smith et al. 2021). It is important to note that while some wetlands may have impoundments or water control structures present, we did not include any wetlands as falling under the category of RSVRs in this thesis. We included drivers that dealt with protected and managed environmental areas (also derived from LAGOS-US GEO), such as superfund site counts, International Union for Conservation of Nature (IUCN) managed habitat percentage, and IUCN reserve percentage to understand if human management and conservation (i.e., habitat protection efforts) impact breeding waterfowl populations. LAGOS-US LOCUS contains additional variables that are likely to influence waterfowl populations, such lake morphometry (e.g., total area, island area), as well as lake and stream connectivity (Cheruvilil et al. 2021, Smith et al. 2021; Figure 3). We also used LAGOS-US LANDSAT, which provides predicted Chl-*a* values based on satellite imagery for lakes  $\geq 4$  ha from 1984 to 2019 on cloud-free days (Hanly et al. forthcoming). We

selected matching Chl-*a* data (Hanly et al. forthcoming) and used the grand mean Chl-*a* data values in order to have one value per lake. Unfortunately, only 38% of lakes (n = 135) had these data. Summary statistics for these continuous predictor variables (drivers) are in Table 1.



**Figure 10.** Map of LAGOS-US RESERVOIR and corresponding histograms showing the locations and class distribution of 137,465 lakes  $\geq 4$  ha as NL (purple, n = 73,053), RSVR\_A (orange, n = 61,042), or RSVR\_B (green, n = 3,370) in the conterminous United States. ‘RSVR\_A’ refers to lakes that are likely human-made or human-altered by a large water control structure; ‘RSVR\_B’ refers to lakes that are likely human-made based on isolation and a shape rare in natural lakes. It should be noted that this dataset had only one RSVR\_B value, and so RSVR\_A and RSVR\_B classes were merged. From: Rodriguez et al. 2023.



**Figure 11.** (A-E) Cartoon depicting the four lake connectivity classes in LAGOS-US RESERVOIR (A; top) and aerial images of the four classes used in this study (bottom; B-E). Image attribution: Esri, DigitalGlobe, GeoEye, i-cubed, USDA FSA, USGS, AEX, Getmapping, Aerogrid, IGN, IGP, swisstopo, and the GIS User Community. Symbols for diagrams courtesy of the Integration and Application Network ([ian.umces.edu/symbols](http://ian.umces.edu/symbols)) (Figure adapted from Cheruvilil et al. 2021).

<b>Predictor Variable (units)</b>	<b>Mean</b>	<b>Standard Deviation</b>	<b>Minimum</b>	<b>Maximum</b>
<b>Lake Total Area (ha)<sup>b</sup></b>	1231.5	10622.0	4.1	121898.7
<b>Lake Island Area (ha)<sup>b</sup></b>	123.9	1248.7	0.0	14365.2
<b>Lake Mean Chlorophyll-<i>a</i> (ug/L)<sup>*,c</sup></b>	10.1	8.9	2.2	54.4
<b>Lake Shoreline Development<sup>b</sup></b>	2.1	1.0	1.2	6.4
<b>WS Road Density (m/ha)<sup>a</sup></b>	42.3	35.7	0.0	182.8
<b>WS Dams (nsqkm)<sup>a</sup></b>	0.1	0.2	0.0	1.7
<b>WS Wetlands (%)<sup>a</sup></b>	13.1	18.5	0.0	100.0
<b>WS Superfund Sites (n/sqkm)<sup>a</sup></b>	0.0	0.0	0.0	0.1
<b>WS IUCN Habitat Species Management (%)<sup>a</sup></b>	0.8	8.2	0.0	95.3
<b>WS IUCN Nature Reserve (%)<sup>a</sup></b>	0.0	0.0	0.0	0.0
<b>WS Cultivated Crop (%)<sup>a</sup></b>	2.9	7.9	0.0	48.0
<b>WS Terrain Ruggedness Index<sup>a</sup></b>	2.2	1.4	0.2	7.7
<b>HU12 Baseflow Index (%)<sup>a</sup></b>	52.0	8.6	34.5	73.0
<b>HU12 Mean Temperature (degrees Celsius)<sup>a</sup></b>	9.9	2.1	3.1	13.9
<b>HU12 Precipitation (mm/year)<sup>a</sup></b>	1187.2	98.5	862.4	1524.2
<b>HU12 Runoff (mm/year)<sup>a</sup></b>	569.3	97.7	263.8	1012.7

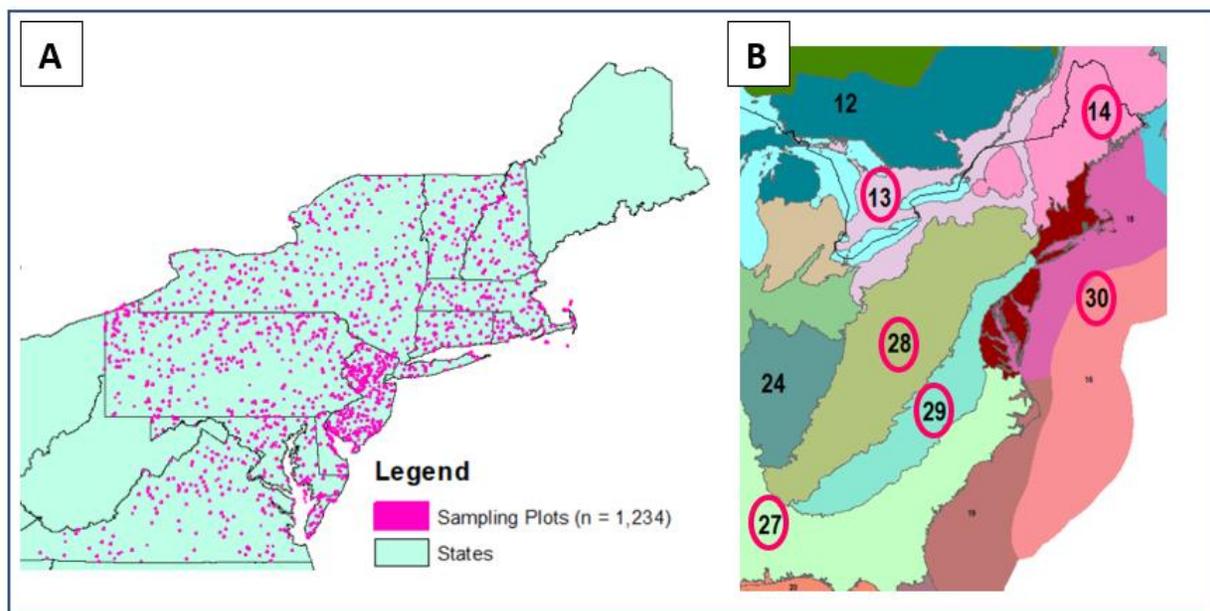
**Table 4.** Summary statistics (mean, standard deviation, range) of the non-transformed, continuous predictor variables included in models. These statistics were quantified for each lake (area, island area, mean Chl-*a*, lake shoreline development factor, or SDF), each lake watershed (WS; wetlands, dams, roads, cultivated crops, terrain ruggedness index, superfund site, IUCN nature reserve, IUCN habitat management), or the HU12 (USGS Watershed Boundary Dataset; Seaber 1987) for when the data source was too coarse (baseflow index, runoff, mean temperature, precipitation). Note that for wetlands, we combined emergent and woody wetland data. N = 135 study lakes with waterfowl and Chl-*a* data. Data are from LAGOS-US GEO (<sup>a</sup>), LOCUS (<sup>b</sup>), and LANDSAT (<sup>c</sup>).

### Study Species

Waterfowl data came from the Atlantic Flyway Breeding Waterfowl Survey (AFBWS) obtained from the United States Fish and Wildlife Service (USFWS) via Anthony Roberts (pers comm). This survey was designed to estimate the breeding population sizes of waterfowl species and includes ten species and an ‘Other Species’ class of unidentified waterfowl (Table 2).

SPECIES	COMMON NAME (ABBREVIATION)
<i>Lophodytes cucullatus</i>	Hooded Merganser (HOME)
<i>Mergus merganser</i>	Common Merganser (COME)
<i>Anas platyrhynchos</i>	Mallard (MALL)
<i>Cygnus olor</i>	Mute Swan (MUSW)
<i>Aix sponsa</i>	Wood Duck (WODU)
<i>Mareca strepera</i>	Gadwall (GADW)
<i>Branta canadensis</i>	Canada Goose (CAGO)
<i>Anas discors</i>	Blue-Winged Teal (BWTE)
<i>Anas carolinensis</i>	Green-Winged Teal (AGWT)
<i>Anas rubripes</i>	American Black Duck (ABDU)

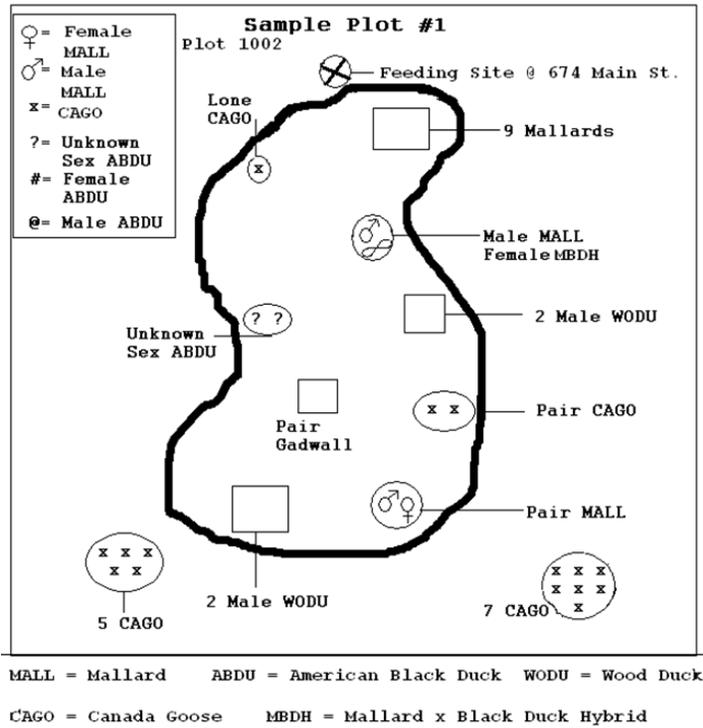
**Table 5.** The ten waterfowl species studied. Data from the Atlantic Flyway Breeding Waterfowl Survey (USFWS). ‘Other Species’ was not included in analysis.



**Figure 12. (A-B)** (A) A map of the northeastern United States depicting the 1,234 1 km<sup>2</sup> plots in the Atlantic Flyway Breeding Waterfowl Survey, from Virginia to New Hampshire. Retrieved from the Atlantic Flyway Breeding Waterfowl Survey Report (2019). (B) A map of the BCRs (Bird Conservation Regions) within the study extent (BCRs 13, 14, 27, 28, 29, and 30). BCR 28 = the Appalachian Mountains, 30 = the New England/MidAtlantic Coast, 14 = the Atlantic Northern Forests, 29 = Piedmont, 13 = the Lower Great Lakes/St. Lawrence Plain, and 27 = the Southeastern Coastal Plain. BCRs utilized in this study are circled in pink.

The AFBWS provides both count and estimated population data from the years of 2000 to 2021. These data span 11 states (Connecticut, Delaware, Massachusetts, Maryland, New Hampshire, New Jersey, New York, Pennsylvania, Rhode Island, Virginia, and Vermont) that include 17 Bird Conservation Regions (BCRs) in the conterminous US. This survey was designed by initially selecting 1,476 sampling points among strata that were based on waterfowl densities from the 'Breeding Bird Survey' (BBS) data and on states according to land area (Heusmann and Sauer 1997, 2000). 1,234 1-km<sup>2</sup> plots were randomly selected and surveyed annually (Figure 4). About 20% of the plots were surveyed at dawn and dusk, the others were surveyed during daylight. Each respective plot was surveyed at the same time each day. Total indicated birds (TIBs) and total indicated pairs of birds (TIPs) were recorded for each plot (Figure 5). We use the TIB data since this research focuses on individual birds. We removed all duplicates and took the mean of all sample points that were >0 for each of the ten species so that mean population densities were not zero-inflated. However, we use both the zeros and the means in further analyses.

The ten species in the AFBWS have numerous similarities in terms of habitat preferences, nesting, behaviors, food and foraging, and conservation status. For example, all ten waterfowl species typically prefer habitats that range between bottomland forests, swamps, freshwater marshes, wetlands, lakes, reservoirs, cropland, grassy fields, and prairie potholes (Cornell Lab of Ornithology, 2019). Their diets, although they differ from species to species, typically consist of plants, seeds, fruits, insects, arthropods, fish, frogs, and even small mammals. Whether in forested areas, agricultural and grain fields, artificial nesting structures, or even heavily vegetated shorelines, peninsulas, and small islands, these species will build their nests in proximity to water.

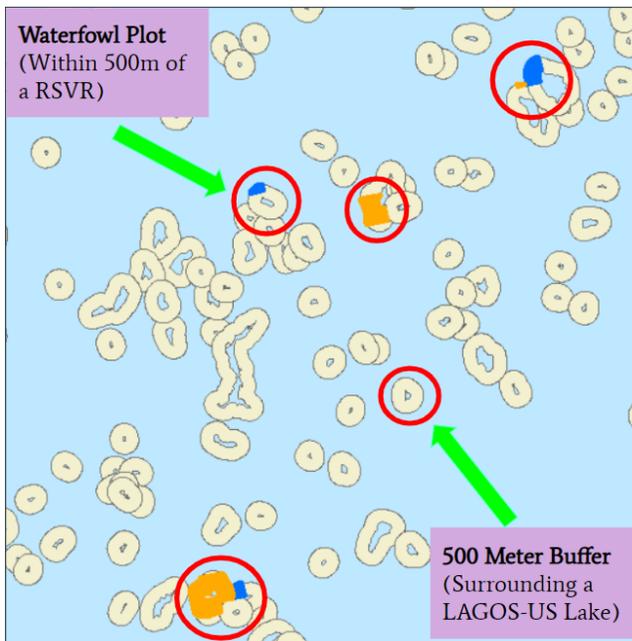


**Figure 13.** An example of a sample 1 km<sup>2</sup> plot from the Atlantic Flyway Breeding Waterfowl Survey containing all observed total indicated birds (TIBs) and all total indicated pairs (TIPs) in the sample plot area (Roberts 2018). See Table 2 for waterfowl abbreviations.

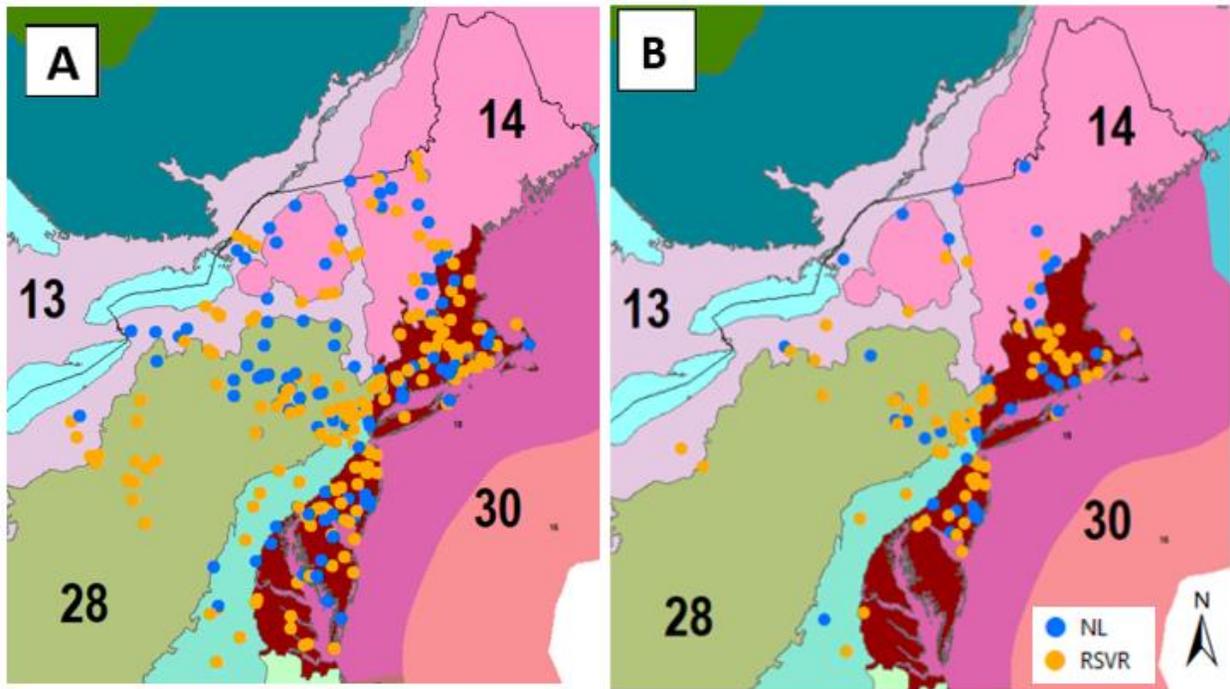
The number of broods produced is typically 1-2 annually, and the broods range from 1-17 eggs, depending on the species in question (Cornell Lab of Ornithology, 2019). In terms of aquatic feeding and foraging behavior, wood ducks, mallards, mute swans, blue-winged teals, green-winged teals, gadwalls, American black ducks, and Canada geese exhibit *dabbling* behavior, or moving their bills around at the surface of the water to obtain food, while common mergansers and hooded mergansers exhibit *diving* behavior (diving beneath the water's surface to obtain nutrients). Of the ten species from the survey, all but one are of least conservation concern (LCC), with the exception being the American black duck that has a relatively low conservation concern (RLCC) (Cornell Lab of Ornithology, 2019). It should be noted that all species included in the AFBWS are hunted, but not during the breeding season (spring) when surveys were performed.

## Data Processing

To compare waterfowl populations between natural lakes and reservoirs, we started by determining how many waterfowl sampling plots fell within 500 meters of a natural lake or reservoir. In ArcMap, we joined the LAGOS-US RESERVOIR to a 500 meter buffer zone polygon layer from LAGOS-US GEO based on the common identifier 'lagoslakeid'. Then, the waterfowl polygon layer with the sampling plots was intersected with the newly joined 500 meter buffer (Figure 6). We also merged these data with the BCRs included in Atlantic Flyway Breeding Waterfowl Survey. The result was 336 unique lagoslakeids composed of 133 NLs and 203 RSVRs, in six BCRs (Figure 7a). Finally, we merged these data with the Chl-*a* data from LANDSAT, resulting in 135 lakes with all driver variables (Figure 7b).



**Figure 14.** A map of the northeastern portion of Pennsylvania containing a collection of the 1 km<sup>2</sup> breeding waterfowl plots that are associated with either a natural lake or reservoir (within a buffer zone distance of 500 meters). The buffers are denoted by the 'doughnut' peach polygons, the natural lakes are depicted in blue, and reservoirs are depicted in orange. Points of intersection (where waterfowl plots fall within 500 meters of a natural lake or reservoir) are circled for visibility.



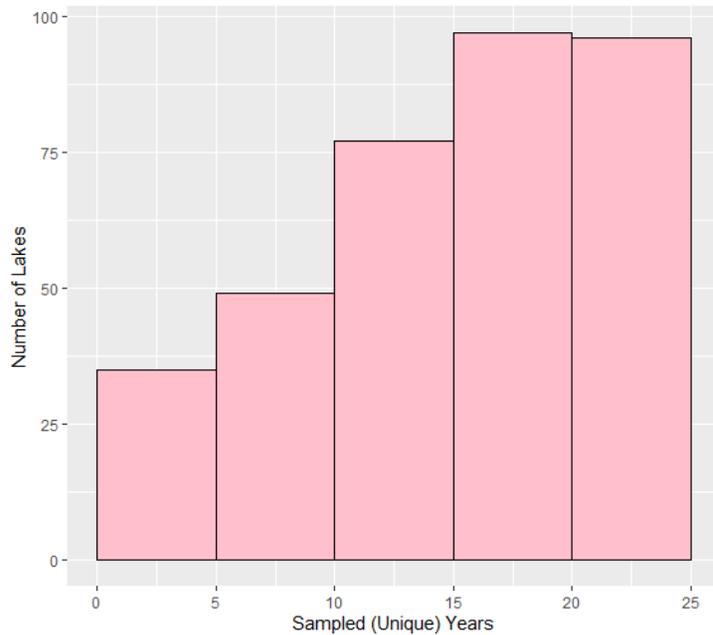
**Figure 15. (A-B)** (A) A map of the northeastern United States and the BCR regions containing the 1 km<sup>2</sup> breeding waterfowl plots that fall within 500m of either a natural lake (n = 133, blue) or reservoir (n = 203, orange). (B) A map of the northeastern United States with the 1 km<sup>2</sup> breeding waterfowl plots that fall within 500m of either a natural lake or reservoir (n = 44, blue) or reservoir (n = 91, orange).

### Analytical Approach

We performed descriptive univariate exploratory analysis to identify missing values and outliers that might unduly affect models, and to understand which predictor variables might be most likely to affect waterfowl. Predictor (driver) variables were either natural log (ln) or natural log +1 (ln +1) transformed to facilitate normal statistical distributions. Correlation matrices were used to determine correlated predictor variables and help us select variables to include in models. No variables with an  $r > 0.65$  were utilized, with the exception of precipitation (mm/year) and runoff (mm/year) ( $r = 0.72$ ), which were included in the final generalized linear model (GLM). We merged the zero-inflated bird data with the finalized predictor data, and applied a two-step modeling process. Our first step was a presence/absence model, designed to show which, if any, bird species were significantly more likely to be present in natural lakes or reservoirs. The presence/absence model was performed on our full sample size of waterfowl lakes (n = 336). Our second model was a generalized linear model GLM, with the chosen family being ‘quasi-Poisson’ to account for abnormal count data (zero-inflated bird TIBs). The GLM was performed on a subset of 135 lakes that had matching Chl-*a* data derived from LAGOS-US LANDSAT.

## RESULTS

We included ten species from the AFBWS that were sampled during the time period of 2000 to 2021. Mean density values ranged from 0.1 (blue-winged teal) to 9.2 (Canada goose) (Table 3). Most lakes were sampled annually, although there were some sampling gaps. For example, ~100 lakes were sampled 15 to 20 years total, the majority of lakes were sampled 10 to 21 years, and 48 lakes were sampled 5 to 10 years total (Figure 8).



**Figure 16.** Bar plot showing frequency of annual sampling for each study lake (n=354, as this was prior to removing 16 rows with complete NA data for waterfowl TIBs) during the 21-year time span. Note that the furthest-right bar includes lakes sampled 20-21 years total since the maximum number of years is 21.

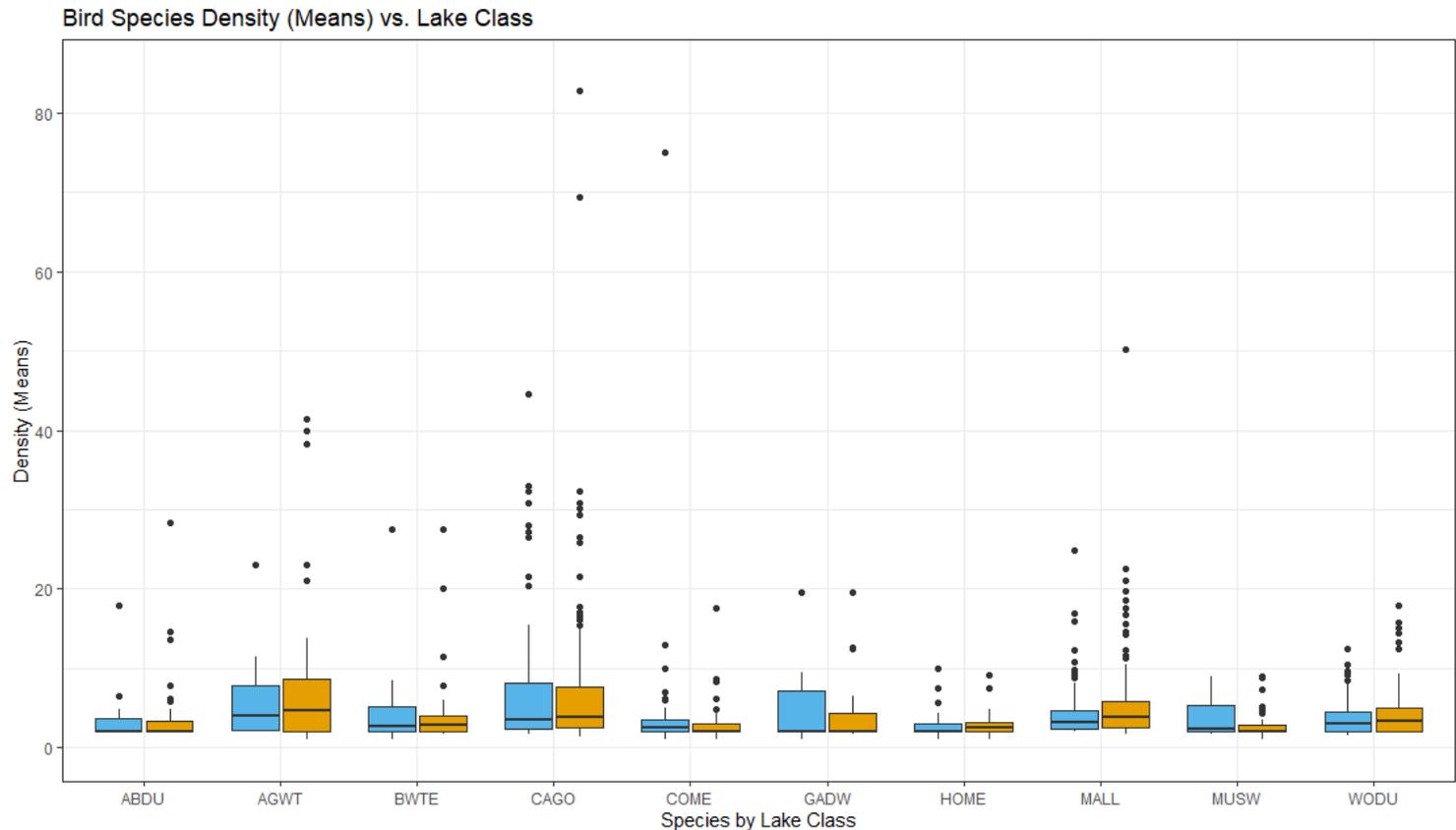
Species	Mean	Standard Deviation	Maximum
American Black Duck	0.8	2.5	28.4
Wood Duck	2.9	2.8	15.2
Blue-Winged Teal	0.1	0.2	0.8
Green-Winged Teal	0.6	1.9	14.6
Mallard	4.1	3.9	50.3
Gadwall	0.2	0.6	6.5
Hooded Merganser	0.2	0.3	1.6
Common Merganser	0.2	0.4	3.1
Canada Goose	9.2	10.3	154.2
Mute Swan	0.3	1.0	6.8

**Table 6.** Summary statistics (mean, standard deviation, maximum) of the non-transformed, zero-inflated waterfowl species response variables for the 336 study lakes that fell within 500 meters of a waterfowl sampling plot. The summary statistics are taken for the mean densities of each of the ten species with zeroes included in the raw TIB count data for each species. Note: Minimum density values are zero (0.0) for all species.

We expected that RSVRs would have significantly higher waterfowl population densities for several, if not all ten, of the waterfowl species in comparison to NLs. Interestingly, t-tests found support for this expectation for only wood ducks and mallards, which had a significantly or marginally significant, respectively, higher density across the 203 RSVRs compared to the 133 NLs ( $p = 0.048$  and  $0.10$ , respectively) (Figure 9). We also did not see any significant differences of the American Black Duck (*Anas rubripes*, RLCC) or the Mute Swan (*Cygnus olor*, LCC) between the lake types. We found similar results when we examined likelihood of species presence in the 336 study lakes. Our presence/absence models indicated that mallards were significantly more likely to be present in RSVRs ( $p = 0.02$ ) as compared to NLs (Table 4). We also found that wood ducks were marginally more likely ( $p = 0.08$ ) to be present in RSVRs and that common mergansers were marginally less likely ( $p = 0.05$ ) to be present in RSVRs as compared to NLs (Table 4).

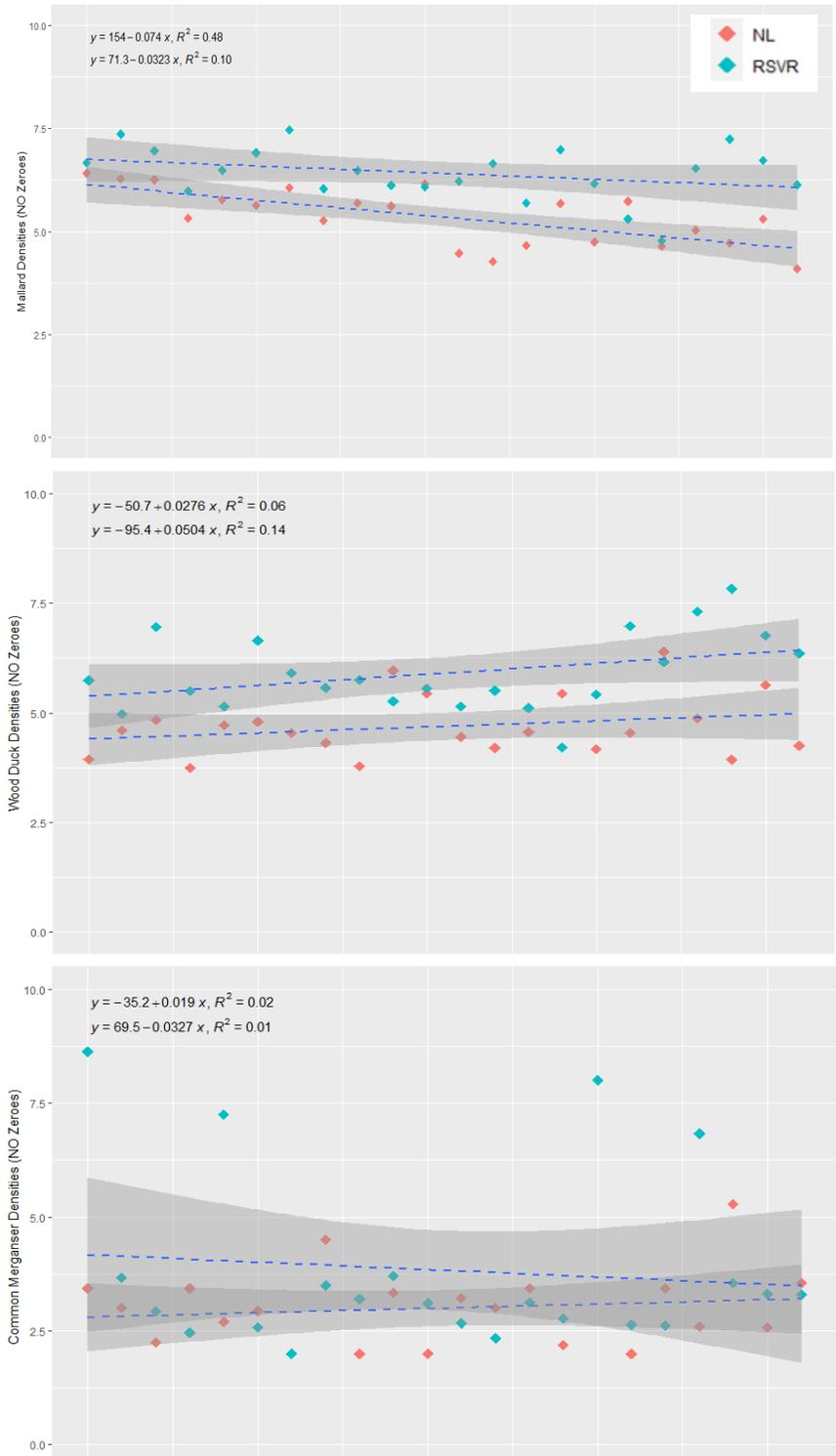
	Presence/Absence Model		
	Wood Duck	Mallard	Common Merganser
<b>Slope</b>	0.8	2.2	-0.2
<b>Total R<sup>2</sup></b>	0.008	0.037	0.008
<b>Lake: RSVR</b>	0.4 (m.s.)	1.1*	-0.5 (m.s.)

**Table 7.** Results of the model of the non-transformed, zero-inflated waterfowl species presence/absence data for the 336 study lakes that fell within 500 meters of a waterfowl sampling plot. Numbers in cells are model coefficients followed by p value of 0.01 or M.S. = marginally significant (i.e.,  $p = 0.051 \geq 0.10$ ).



**Figure 17.** A boxplot of the *non-zero inflated* waterfowl species mean densities by lake class (NL or RSVR) for the 336 study lakes. T-test p-values are shown above the plot. Note: outlier value of 154.2 for CAGO is not depicted for visualization purposes. See Table 2 for waterfowl species abbreviations.

We next examined trends through time for the three species with marginally significant/significant differences in densities and/or likelihood of presence in RSVRs vs. NLs. Our results indicate that mallard population densities decreased slightly in both RSVRs and NLs over the 21-year time span of 2000 – 2021 (Figure 10a). In contrast, wood duck population densities increased slightly in both RSVRs and NLs over the 21-year time span (Figure 10b). Finally, we found that common merganser population densities seem to be heading to a point of intersection across RSVRs and NLs over time, with densities slightly decreasing in RSVRs and slightly increasing in NLs through time (Figure 10c). For all three species, there were higher population densities in RSVRs as compared to NLs.



**Figure 18.** Scatterplots of the *non-zero inflated* waterfowl species mean densities by lake class (NL or RSVR) over the study time period of 2000 - 2021: A) mallard B) wood duck C) common merganser. Regression equations are NL on top and RSVR on bottom, best-fit lines are shown with the dashed line, and gray shading represents the 95% confidence interval.

Finally, we expected that waterfowl populations would be predicted by a variety of drivers including lake type (i.e. NL or RSVR), Chl-*a* concentrations, LULC, climate, connectivity, regional variation, and managed or protected natural areas. We tested this expectation for the same three waterfowl species – wood duck, mallard, and common merganser – and for the subset of lakes with Chl-*a* ( $n = 91$  RSVRs and 44 NLs). Our results indicated that lake type was not significantly associated with these three waterfowl species densities. However, other predictor variables were significant in each a model of each species.

For wood ducks, 29% of the variation in densities was explained by three significant (BCR, runoff, temperature) and three marginally significant variables (lake island area, roads, precipitation) (Table 5). For mallards, 47% of the variation in density was explained by three significant (BCR, Chl *a*, cultivated cropland) and three marginally significant variables (SDF, roads, connectivity). For common mergansers, 46% of the variation in densities was explained by one significant (lake area) and two marginally significant (connectivity, temperature) variables (Table 5). Interestingly, there were no predictor variables that were consistently significant across the three waterfowl species.

	Quasi-Poisson GLM Results		
	Wood Duck	Mallard	Common Merganser
<b>Slope</b>	0.9	1.9***	-1.1
<b>BCR Region</b>	ID: -30*	ID: -28*, -30, (m.s.)	n/a
<b>Lake: RSVR</b>	n/a	n/a	n/a
<b>Chlorophyll-<i>a</i></b>	n/a	0.3**	n/a
<b>Lake Area</b>	n/a	n/a	0.7*
<b>SDF</b>	n/a	0.2, (m.s.)	n/a
<b>Lake Island Area</b>	0.3, (m.s.)	n/a	n/a
<b>Roads</b>	-0.3, (m.s.)	0.2, (m.s.)	n/a
<b>Dams</b>	n/a	n/a	n/a
<b>Superfund Site</b>	n/a	n/a	n/a
<b>Runoff</b>	0.9**	n/a	n/a
<b>Baseflow</b>	n/a	n/a	n/a
<b>Connectivity: Drainage</b>	n/a	0.4, (m.s.)	-1.0, (m.s.)
<b>Temperature</b>	0.6*	n/a	-0.7, (m.s.)
<b>Precipitation</b>	-0.6, (m.s.)	n/a	n/a
<b>Cultivated Cropland</b>	n/a	-0.3*	n/a
<b>Wetlands</b>	n/a	n/a	n/a
<b>TRI</b>	n/a	n/a	n/a
<b>IUCN Habitat Management</b>	n/a	n/a	n/a
<b>IUCN Nature Reserve</b>	n/a	n/a	n/a
<b>Total R<sup>2</sup></b>	0.29	0.47	0.46

**Table 8.** Summary of generalized linear model (GLM) quasi-Poisson results for mean population densities of three species (wood ducks, mallards, common mergansers) of waterfowl as a function of many predictor variables characterized at multiple spatial scales. Models were run on the subset of lakes with Chl-*a* data (n = 135). Numbers in cells are model coefficients followed by p-values at levels of \*\*\* = 0.0, \*\* = 0.001, and \* = 0.01; M.S. = marginally significant (i.e., p = 0.051 ≥ 0.10). ‘n/a’ indicates that a predictor variable was not significant in that model. Three categorical predictor variables were included in models (standard is listed in the predictor variable cell): BCRs (6 Regions; see Figure 7), Lake Class (RSVR or NL), Connectivity (4 Classes; I/H = isolated and headwater lakes; see Figure 3). For these

**Table 8 (cont'd).**

categorical variables, each cell includes any significant coefficients, whether it was + or -, and which classes were significant. TRI = Terrain Ruggedness Index, and SDF = Lake Shoreline Development Factor. Models were performed on standardized variables to aid in coefficient comparisons and transformations were performed when needed to meet statistical assumptions. See Table 1 for units of continuous predictor variables and Table 3 for units of response variables.

**DISCUSSION**

With this research, we sought to understand how waterfowl populations compare between the lake types of NLs and RSVRs. We combined lake, landscape, climatic, and breeding waterfowl data to ask: Do breeding waterfowl population densities differ by lake type?, Are particular species more likely in NLs or RSVRs during the breeding period?, Are breeding waterfowl population densities changing over time and according to lake type?, and What climatic, lake, and landscape factors are associated with differences in breeding waterfowl densities between lake types?

With hundreds of lakes at the macroscale, we were unable to detect differences in presence or density of seven waterfowl species. For the three species with presence and/or density data that differed by lake type (mallard, wood duck, common merganser), mallards and wood ducks were more likely in RSVRs than NLs, and common mergansers were less likely in RSVRs. However, only wood ducks and mallards had higher densities in RSVRs. These three species also showed some change in population density over the 21-year temporal extent, but that change also depended upon the species. Finally, we found that a combination of lake, landscape, and climate driver variables, but not lake type, predicted population densities of these three waterfowl species. Taken together, these results demonstrate the importance of lake type, Chl-*a* concentrations, region, and a variety of morphological, landscape, and climatic variables for understanding waterfowl populations at broad scales.

**Waterfowl Presence and Densities in Reservoirs**

We initially expected to see a greater likelihood of waterfowl presence and significantly higher population densities in RSVRs as compared to NLs. These expectations were based on RSVRs having poorer water quality when compared to NLs, with higher concentrations of TP and Chl-*a*, and subsequently lower WC (Domka, thesis chapter 1) and the fact that lake eutrophication may produce desirable habitat space for many waterfowl species (Hoyer and Canfield 1994, Kauppinen and Väänänen 1999). Additionally, we know that waterfowl use RSVRs for breeding, nesting, and feeding (Owen and Black 1990). Interestingly, we found no difference in likelihood of presence and population densities between RSVRs and NLs for seven waterfowl species. However, this result may be a function of limitations associated with the survey data. The AFBWS sample sizes were often low, especially for hooded mergansers, common mergansers, mute swans, gadwalls, blue-winged teals, and green-winged teals, leading to large standard errors around count data. Therefore, we may not have had sufficient power

to detect waterfowl differences by lake type. Another possibility is that lakes in general are not the primary desired habitat of these species and the open water associated with lakes (i.e., RSVRs or NLs) is used typically for resting purposes only.

For the three species (wood ducks, mallards, common mergansers) that differed by lake type, our results were generally consistent with our expectations and make sense in light of their biology. The wood duck is commonly found along freshwater ecosystems of many sizes and of both moving and still water, including streams, creeks, and even larger rivers (Cornell Lab of Ornithology, 2019). However, wood ducks feed on aquatic plants such as duckweed (*Lemnoideae spp.*), which is typically found in still and eutrophic environments, such as RSVRs, and tend to exhibit higher energetic demands compared to other species of waterfowl (Cornell Lab of Ornithology, 2019). Therefore, it is not surprising that this species of waterfowl would prefer RSVRs over NLs for biological activities such as breeding, nesting, and feeding.

Mallards can thrive in a variety of habitats and feed on aquatic vegetation, oftentimes being found foraging in the riparian zone of lakes or rivers (Cornell Lab of Ornithology, 2019). Although mallards are said to be ‘susceptible’ to changes in their habitat, such as poor water quality, pesticides, higher nutrient levels (Cornell Lab of Ornithology, 2019) we found higher mallard densities in RSVRs, which generally are more nutrient-rich. It may be that mallards are deterred once past a threshold of nutrient pollution that our study systems did not approach. In fact, mean Chl-*a* in our systems was 10.3 ug/L (range of 2.2-54.5 ug/L), indicating that these systems are generally eutrophic rather than hypereutrophic (Carlson 1977).

In presence/absence models, common mergansers were less likely to be present in RSVRs compared to NLs. However, they did *not* have significantly higher densities in RSVRs, indicating that common mergansers were present, but in low densities in RSVRs. Common mergansers tend to winter on larger lakes and forage in large, clear aquatic environments, which suggests that this species may have a preference for oligotrophic environments rather than eutrophic ones (Cornell Lab of Ornithology, 2019). As these piscivorous birds are fairly high up on the aquatic food chain, it is sometimes used as a bioindicator of environmental health and may provide information as to the amount of pesticides, nutrients, and toxins in an ecosystem (Cornell Lab of Ornithology, 2019). Perhaps common mergansers prefer NLs rather than RSVRs because RSVRs have higher nutrient levels (Domka, thesis chapter 1) that can be caused by agricultural runoff.

### **Population Densities in Reservoirs Through Time**

We found some change in population density over the 21-year temporal extent, but those change depended upon species and, sometimes, lake type. Mallard populations decreased and wood ducks increased in both RSVRs and NLs from 2000-2021, whereas common mergansers increased in NLs and decreased in RSVRs. However, with the exception of mallards in RSVRs, the trends found were not

particularly strong through time (i.e., relatively small slope estimates and  $R^2$  values). Other studies have also documented population changes in waterfowl in recent years. For example, a study by Banks and Springer (1994) found that waterfowl population surveys indicated declining numbers of ducks, and that hunting, habitat loss, and drought conditions have been primarily responsible for these significant losses. Furthermore, a study by Niemuth et al. (2014) found that waterfowl experienced both population declines as well as increases depending on the time of year, and that precipitation, temperature, and longitudinal and latitudinal measurements were important in predicting waterfowl populations. These findings are consistent with our results for mallard breeding populations, as we found that their respective populations decreased in both lake types over the 21-year temporal extent. Interestingly, we saw the opposite trends for common mergansers and wood ducks, with increases for both species with the exception of common mergansers decreasing in RSVRs. Finally, according to a Ducks Unlimited waterfowl survey (2022), a 12% decline was observed in breeding duck populations compared to the year 2019 (Zimpfer et al. 2022). These drastic changes were attributed to prairie drought and habitat degradation. Interestingly, our results did not indicate complete population declines, and population decreases were typically dependent on both species and lake type. Thus, when considering waterfowl conservation and management practices, it is critical to not only consider ecological drivers like precipitation, temperature, and wetland coverage (as many of these studies suggest), but to evaluate lake type itself and how specific waterfowl species may be more or less adaptable to NLs or RSVRs.

RSVRs are known to have poorer water quality and higher nutrient concentrations than NLs (Domka, thesis chapter 1), which could underly these opposing trends for the common mergansers, a species that may prefer NLs as compared to RSVRs. They tend to forage and winter in oligotrophic water bodies, and are sensitive to factors associated with declining overall water quality (Cornell Lab of Ornithology, 2019). Future research should examine whether the decreasing trends in mallards are related to concomitant decreases in water quality. Interestingly, we found wood duck populations increasing through time for both lake types. Therefore, future research is needed to determine whether these waterfowl population changes remain and what might be causing them.

### **Drivers of Waterfowl in RSVRS**

The variables that predicted wood duck populations were: BCR (region), lake island area, roads, runoff, temperature, and precipitation. The variables that predicted mallard populations were: BCR (region), Chl-*a* concentrations, SDF, roads, cultivated crop, and lake connectivity class. Finally, the variables that predicted common merganser populations were: lake area, temperature, and lake connectivity class. Interestingly, there were no driver variables that were significant across all three species. In addition some of the variables that we most expected to drive population densities were not

significant (i.e., lake type, managed and conserved lands). Below, we talk about a few variables in particular that may be highly influential in waterfowl population success.

We found that higher Chl-*a* concentrations were associated with higher mallard population densities, but had no significant effect on wood duck or common merganser population densities (Table 5). Chl-*a* is a measure of the amount of floating algae in aquatic ecosystems (Björn et al. 2009) that is positively associated with nutrient levels (Prairie et al. 1989) and negatively associated with water quality, all of which affect waterfowl populations (Hoyer and Canfield 1994, Kauppinen and Väänänen 1999). Breeding waterfowl populations depend on nutrient levels for success (Suter 1994), and aquatic bird populations were shown to increase as water bodies became more eutrophic, likely because productive water bodies have greater food resources for wildlife (Hoyer and Canfield 1994). Our model reflects higher population densities of wood ducks as runoff increases, and higher runoff is associated with eutrophic habitats (Khan and Mohammad 2014). Interestingly, waterfowl are capable of degrading water quality through unintentional import of nutrients (Hoyer and Canfield 1994, Manny, Johnson, and Wetzel 1994), leading to a bi-directional linkage between waterfowl and nutrients. Our results may suggest that the relationship between Chl-*a* and waterfowl population densities is not a linear one, which mirrors some macroscale studies that have shown that Chl-*a* has a non-linear relationship with TP (Filstrup and Downing 2017, Wagner et al. 2014). Rather, there may be a point at which increased Chl-*a* concentrations are beneficial to waterfowl (providing food and energy for nesting and breeding), and past this point, the rising Chl-*a* levels become excessive and act as a deterrent to some species. However, more research would be needed on this subject to see if any waterfowl species experienced population density decreases in response to increased Chl-*a* levels. Overall, success of breeding waterfowl populations in the presence of nutrient pollution is likely due to biological differences and a species' individual ability to tolerate poor water quality.

Previous research (Zhao et al. 2016, Zimmerman et al. 2015) has highlighted the importance of using BCRs in waterfowl habitat management and for forecasting trends in waterfowl populations. Our results support this assertion and provide information regarding specific species in relation to BCRs. We saw lower population densities for mallards in the Appalachian Mountains, and lower population densities for both wood ducks and mallards in the New England/Mid-Atlantic Coast (BCRs 28 and 30, respectively). The New England/Mid-Atlantic Coast region (BCR 30) has both dense human populations with high levels of pollution and is characterized by loss of the submerged aquatic vegetation (SAV) that these waterfowl rely on for breeding and offspring survival (Owen and Black 1990). Furthermore, wintering and migrating waterfowl are known to frequently use both estuarine complexes and embayments (a recess in a coastline that forms a bay), which are both common marine features found in this region (Steinkamp and Venture 2008). Interestingly, these habitats are susceptible to eutrophication

and cyanotoxins, which can lead to extensive waterfowl mortality, which may be contributing to population declines of certain species (Wurtsbaugh et al. 2009). Finally, the landscape of this region has undergone significant changes due to increased urbanization, forestry, and agriculture, and one of its primary threats to waterfowl is habitat fragmentation (Steinkamp and Venture 2008). Habitat degradation can affect waterfowl (Xu et al. 2019), and increasingly urban environments can disrupt migratory patterns and cause population fluctuations (Avilova and Eremkin 2019, Staniforth 2002).

We also saw declining population densities for wood ducks in the Appalachian Mountains (BCR 28). The Appalachian Mountains region is characterized by large wetland complexes and heavily forested areas, all of which are utilized by waterfowl to some degree (Cornell Lab of Ornithology 2019, McKinstry and Anderson 2002). In this region in particular, the wetland complexes present are typically used for wood duck breeding and habitat. Destruction and fragmentation of habitat space, as well as large areas of land devoted to agricultural use, could be contributing to wood duck population declines (Dwyer 1970, Xu et al. 2019). Furthermore, dabbling ducks (such as the wood duck) have been found to prefer nonagricultural lands to agricultural ones, further reinforcing the idea that wood ducks may be sensitive to the massive amount of habitat disruption in the Appalachian Mountain region (Dwyer 1970). Finally, the Appalachian Mountain region is known to have numerous headwaters of major river systems that are used by waterfowl during migratory events (Steinkamp and Venture 2008). These headwater habitats are susceptible to pollution, fragmentation, and wetland disturbance or destruction, further jeopardizing potential wood duck habitat and factors needed for their biological success (Barry and Foy 2016). This complex discussion of the role of ecological factors and individual regions further reinforces the idea that the relationship between breeding waterfowl population densities and ecological drivers is not a simple one, and that many factors likely work in tandem to produce certain patterns.

Many past studies have suggested that weather and climate affect waterfowl populations. In our models, higher mean temperatures were associated with larger wood duck population densities, and smaller populations of common mergansers (Table 5). These species-dependent results are not entirely unsurprising, because climate change has very complicated effects on species, and waterfowl are particularly sensitive to changes in climatic factors, serving as bioindicators of changing climatic conditions (Avilova and Eremkin 2019, Fernández et al. 2005, Lehikoinen and Jaatinen 2013). For example, rising global temperatures are said to contribute to increased evapotranspiration and greater incidence of drought conditions, leading to loss of both wetlands and waterfowl species (Sorenson 1998) and climate changes can produce earlier breeding events as well as delayed migration events (Lehikoinen and Jaatinen 2013). More specifically, wood duck migration distances were found to be influenced by precipitation levels, and migrations typically ended further south when temperatures were cooler than normal (Hepp and Hines 1991). Yet another study found that common mergansers were moderately

vulnerable to changes in climate, specifically precipitation levels (Siegel et al. 2014). Finally, common mergansers in a nature reserve had a later springtime arrival, likely due to recent changes in annual air temperatures (Bobretsov et al. 2017).

Although we did not initially expect morphometric variables to be predictive of waterfowl population densities, we found larger common merganser populations with greater lake area and larger wood duck populations with larger lake island area (Table 5). Common merganser species abundance has been shown to increase with growing lake area, particularly for this piscivorous birds (Suter 1994). Previous research has also shown that waterfowl use islands as refuges from disturbance by mammals or other birds, and as a source of water, food, and nesting cover (Hammond and Mann 1956). Furthermore, waterfowl species were found to have high reproductive success when island habitat was available (Lokemoen et al. 1984). Thus, it is unsurprising that lakes with larger island areas would serve as attractive habitat to wood ducks.

Furthermore, we expected lake connectivity class to be predictive of waterfowl populations. Our results demonstrated higher mallard populations and lower common merganser populations in ‘Drainage’ lakes, which are connected to upstream streams. Interestingly, it has been found that water bodies that are more hydrologically connected had greater waterfowl use (Murphy et al. 1984). **Research Limitations**

There are a few limitations to our research that restrict the application of our results. First, there may be additional predictor variables that drive waterfowl populations that we did not study. For example, we know that lake depth is an important predictor of waterfowl (Hoyer and Canfield 1994, Murphy et al. 1984, Nilsson and Nilsson 1978). However, we were not able to include lake depth as a driver variable in our research, as only about 25% of the waterfowl lakes had depth data associated with them. Second, we know that not all RSVRs are the same. In fact, there is a wide range of what constitutes a RSVR, from a dammed major tributary for hydropower to the simple definition of “[hu]man-made lakes” (Lehner and Döll 2004, Rodriguez et al. 2023). Therefore, it would be interesting to go beyond the dual lake classification system of NL vs. RSVR, and delve into the two types of RSVRs (RSVR-A and RSVR-B), or further classify RSVRs by other important features such as human disturbance. The two RSVR types in LAGOS-RESERVIOR differ based on water control structure presence (RSVR-A) vs. angularity (RSVR-B; Rodriguez et al. 2023). Since lake morphometry (i.e. lake area, SDF, island area) has been shown to significantly influence waterfowl population densities, angularity of a given NL, RSVR-A, or RSVR-B could certainly influence breeding birds and their behaviors. Therefore, a more involved study that looks at waterfowl preference for one RSVR type over the other could lend insight into waterfowl breeding, nesting, and feeding behaviors at the macroscale. Our results were also limited by the wetland driver variable, given that we only had data indicating percentage of wetland coverage,

rather than regional, or more detailed, wetland data. We know that waterfowl use wetland environments for essential survival activities such as feeding and foraging, habitat space, and general refuge (Shaw and Fredine 1971, Stafford et al. 2011). Furthermore, constructed, or artificial, wetlands are oftentimes erected in order to increase the availability of waterfowl breeding habitat, and wetlands complexes are known to provide critical resources to breeding and migrating waterfowl such as dependable food and water availability (McKinstry and Anderson 2002). Therefore, future research should further examine the impact of wetlands and wetland availability on breeding waterfowl populations, and should attempt to understand if this driver ties in with lake type in any way. Additionally, we would need to further analyze our ecological driver model to understand whether or not the model itself is overparameterized (i.e. too many predictor variables for a sample size of only 135 lakes). This potential overparameterization could be affecting which variables are significantly driving breeding waterfowl populations. Finally, it would be interesting to study waterfowl species that are of greater conservation concern to understand their preference for (or lack thereof) RSVRs and whether their responses to changing climate and water quality conditions is different from the relatively stable species we study here.

## **CONCLUSION**

To our knowledge, this was the first project to combine lake, landscape, climatic, and waterfowl data to ask questions about what drives waterfowl populations in hundreds of lakes at the macroscale. In particular, we build understanding about the influence of lake type on waterfowl populations. We found that lake type played a role in understanding the likelihood of presence and/or population densities of three species of waterfowl, which can inform the management and conservation actions needed for breeding waterfowl populations of mallards, common mergansers, and wood ducks in the Atlantic Flyway region. We also saw some modest changes in populations densities over the past 21 years, although that varied among the three species and sometimes by lake type. Finally, we found that a variety of lake, climate, and landscape predictor variables significantly impacted waterfowl populations densities (e.g., Chl-*a*, morphometry, region, land use, climate). Therefore, these drivers should be accounted for when future decisions are made regarding the health and conservation of waterfowl and managing aquatic ecosystems for waterfowl populations.

Waterfowl can be reflective of and sensitive to changes in water quality (Fernández et al. 2005), landscape (Avilova and Eremkin 2019, Staniforth 2002), and climate (Avilova and Eremkin 2019, Lehtikoinen and Jaatinen 2013, Sorenson et al. 1998), and depend on a variety of freshwater characteristics for their success in breeding and survival (Suter 1994). Although there was a suspected bi-directional linkage between waterfowl and nutrients (Hoyer and Canfield 1994, Kauppinen and Väänänen 1999, Manny, Johnson, and Wetzel 1994), it was unknown how breeding waterfowl population densities

compared between NLs and RSVRs, if their presence/absence likelihood differed by lake type, if their populations gravitated towards a specific lake type over time, and if specific ecological drivers were influencing their population densities. It is imperative that researchers continue to study waterfowl at the macroscale and take into consideration lake type, along with other lake, climatic, and landscape characteristics that affect waterfowl populations.

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